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A quantitative trait response evaluation to selection in the BS13(S) maize (Zea mays L.) population

Clinton J. Turnbull
Iowa State University

A quantitative trait response evaluation to selection in the BS13(S) maize (*Zea mays* L.) population

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Clinton J. Turnbull

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Program of Study Committee:
Kendall R. Lamkey, Major Professor
Theodore B. Bailey
E. Charles Brummer
Jode Edwards
Jean-Luc Jannink

Iowa State University

Ames, Iowa

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Graduate College
Iowa State University

This is to certify that the doctoral dissertation of

Clinton J. Turnbull

has met the dissertation requirements of Iowa State University

Signature was redacted for privacy.

Major Professor

Signature was redacted for privacy.

For the Major Program

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Abstract

Seven cycles of half-sib recurrent selection were conducted in the BSSS maize population followed by ten cycles of S_2 progeny recurrent selection. The population under S_2 progeny recurrent selection is formally known as BS13(S). The selection criteria have always placed importance on high grain yield, low grain moisture, and reduced plant lodging. Two evaluations estimating the response of multiple agronomic traits in multiple response units including the population sampled at $F_{IS} = 0$, $F_{IS} = 0.5$, and $F_{IS} = 0.75$ levels of inbreeding, and multiple testcrosses of the population were conducted. The average response of grain yield in the $F_{IS} = 0.5$ and $F_{IS} = 0.75$ response units (i.e. inbred response units) of the population are significantly greater than the average responses in both the panmictic population and multiple testcrosses of panmictic population. There is no statistical grain yield response to selection in the $F_{IS} = 0$ response unit (panmictic population). A testcross of the panmictic population to BS13(S)C_0 has an average response greater than the panmictic population indicating that the limited response in the $F_{IS} = 0$ response unit is not likely due to random genetic drift, however, the allelic frequencies are diverging from the progenitor population. Favorable responses have been observed for root lodging in all of the response units however, a limited response for stalk lodging exist. The response of grain moisture is inconsistent between the two evaluations likely as a result of inconsistent selection practices and the difficulty to select for this trait. We hypothesize that the most important reason for the realized lack of response in the panmicitc population is due to a low inbred-outbred correlation and may be caused by an overdominant-like gene action within this population. To avoid the necessity for assumptions about gene action controlling the traits in maize and importance of additive and non-additive effects, the genetic gain equation must be developed

in relation to the selection unit and target response unit (i.e. S_1s, S_2s, half-sibs, or full-sibs). This dissertation supports both the genetic gain equations reported by Wardyn (2006) and the hypothesis of overdominant-like gene action in this population reported by Edwards and Lamkey (2002).

CHAPTER 1. INTRODUCTION

Plant breeding is the art and science of developing genetically improved plants (Fehr, 1991 p.1). Any person that has been involved in the conscious selection of plants with favorable characteristics versus accepting whatever nature provides has actively taken a role in plant breeding. Likely more attempts to improve plants for favorable characteristics have failed than those that have succeeded. Methods for crop improvement are often based on current theory. The hypothesized superior methods from theory must then be tested to determine if the proposed selection methods are effective and in-fact superior to previous methods.

Mass selection is an easy method of crop improvement and the oldest method of plant breeding. Prehistoric people used this method when they looked for superior plants to harvest. Superior plants likely had more harvestable grain due to shattering resistance and had favorable taste and milling qualities. Early maize farmers would annually select and save the best ears. The most desirable ears were shelled and a bulk of the seed was used to plant the next season's crop. The seed crop was chosen based solely on the phenotype of individual ears of corn. In 1903 Wilhelm Johannsen, Willet M. Hays, and earlier Professor Hjalmar Nilson demonstrated that selection should be based on the entire plant, not just the flower or individual plant parts (Poehlman and Sleper, 1995). Louis Leveque de Vilmorin is credited for development and use of the progeny test as a successful means of crop improvement. The selected plants in this scheme are based on the performance of the progeny, versus the individual plant. The progeny test scores an individual based on its progeny's phenotype versus its own. The progeny test has been monumental in the advance

of plant breeding and is the basis for current plant breeding programs. The type of progeny refers to the relationship of the progeny with one another and in many plant species many family structures may be readily developed.

Maize breeders in the early part of the 20th century developed several methods for developing improved maize cultivars (Hull, 1952; Sprague, 1946; Hull, 1945; Jenkins, 1940; Jenkins, 1935; Hays and Garber, 1919; Jones, 1918; Shull, 1909; East, 1908). The methods varied based on the types of progeny developed for evaluation, the type of progeny used for successive breeding, and how the progeny were bred in successive generations. These methods were largely deemed successful or not, based on realization of improvements from the original populations and/or ability to maintain seed stocks of similar performance.

Genetic variation is a population parameter that is partitioned into variation within and variation among the progeny families. The relationship of progeny developed in a breeding program determines the proportion of genetic variation within progeny families and among progeny families. Different forms of gene effects may control the expression of characteristics to include: dominant, additive, overdominant, epistatic, and combinations of any level of all four (Sprague and Eberhart, 1977). By using the various partitions of within and among progeny genetic variances expected from various types of progeny along with considerations for types of gene action, theoretically superior recurrent selection methods were predicted (Comstock, 1964).

Recently with the advances in the selection theory (Holland et al., 2003), a more complete genetic gain prediction model has been developed (Wardyn et al., 2006) than that of Comstock's (1964). This advancement is based largely on completely defining covariance parameters within a population and applying them in the heritability estimate used in the

prediction equation. Specifically, the covariance of importance is that of the progeny evaluated in the selection method (selection unit) with the progeny evaluated for response to selection (response unit). Previously, it was known that the heritability in the prediction equation was often biased. Hallauer and Miranda (1988) published a bias term accounting for the biased deviation from additive genetic variance. However due to unique genetic designs required to estimate this term, it is often inaccessible and the additive genetic variance was used alone in the heritability estimate.

The self progeny recurrent selection method, also referred to as inbred progeny recurrent selection (Fehr, 1991), is the method that Comstock (1964) argued was the superior population improvement method. This method has been evaluated and concluded to be ineffective for improvement of grain yield in multiple maize populations (Lamkey, 1992; Iglesias and Hallauer, 1989; Tanner and Smith, 1987; and Horner et al., 1989). Additionally, the latter two studies indicate, via direct comparisons of selection methods, that inbred progeny selection is not superior to other methods of selection. Each of these studies evaluated the panmictic population as the response unit because the panmictic population is the population unit to be improved in a recurrent selection program (Fehr, 1991).

With the clarification of heritability estimates to be used in the genetic gain equation (Holland et al., 2003), referencing the covariance of selection units and response units versus other variance estimates, it has become of interest to measure the realized response of various response units in a selection program. The response units of most interest are the panmicitic population and a random sample of individuals self pollinated to a given level of inbreeding from a population having undergone several recurrent cycles of inbred progeny selection.

The focus of this dissertation is to measure the realized responses of various response units from multiple cycles of the BS13(S) maize population. Specifically, average responses regressed across cycles of selection to remove random deviations of the population will be investigated along with specific patterns of response for each of the response units. Additionally, the measure of realized response in proportion to the effort of selection (realized heritability) will be investigated. In so doing support may be added to the development of the genetic gain equations published by Wardyn et al. (2006) giving the breeder better tools to aid in choosing truly superior selection methods for germplasm with similar genetic population parameters as those investigated here.

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CHAPTER 2. LITERATURE REVIEW

Crop Improvement Methods

Shull (1908) described the genetic structure of open pollinated varieties of maize as complex populations of hybrids. He additionally outlined a breeding method, based on the genetic structure he proposed, to identify and manage seed stock of high performing maize cultivars (Shull, 1909). The genetic improvement in maize yields in the corn belt between the 1930 and 1960 were attributed to double cross hybrid methodology (Troyer, 2001) developed by Jones (1918, p.60), to capitalize on Shull's (1910) proposals. However neither Shull (1910) nor Jones (1918) described a means for continued crop improvement. Their breeding methods merely identify superior genotypes with the ability to reproduce only the best genotypes for seed production.

To fill this void, recurrent selection was proposed as a breeding method from which continued cultivar improvement may be made (Jenkins, 1940). The utility of recurrent selection is very flexible in that it may be used to develop improved cultivars directly (Jenkins, 1940) or used to develop inbred lines for use in hybrid combinations (Hull, 1945). The objectives of recurrent selection are to maintain genetic variability while gradually increasing the mean performance of a population for desired traits (Hallauer, 1992). Recurrent selection is a cyclical process which has three stages: 1) sampling progeny from a population to develop progeny families, 2) evaluation of progeny families, and 3) genetic recombination of superior progeny to form a new population for continued cycles of selection (Hallauer, 1992). Recurrent selection as a perpetual breeding method dramatically

increases the chances of identifying superior progeny versus non-recurrent breeding methods such as those outlined by Shull (1910) and Jones (1918) (Hull, 1945).

Theoretical Response to Selection

Early Theory

Because plant and animal breeding is a never-ending process, breeders are interested in quantifying success from previous breeding efforts to aid in choosing the most appropriate breeding methods and breeding populations for which to continue breeding (Lush, 1936). Lush (1945) hypothesized that predictions for future improvement from heritable genetic effects should be possible. In part, evaluations of breeding populations, have been used to determine the proportion of total phenotypic variance, σ^2_{Ph}, that is heritable, σ^2_A/σ^2_{Ph} (Lush, 1936 p. 182). This proportion has been defined as heritability and was so defined in an attempt to predict which characteristics might be able to more easily be changed through future breeding efforts in a particular population (Lush, 1940). In retrospect, the realized heritability is the proportion of the observed response to the selection differential (Lush, 1945). The selection differential is the difference between the mean of the selected individuals and the mean of all individuals. The realized response is the difference between the mean of the progeny derived from selected individuals and the population mean (Lush, 1940). Nyquist (1991) emphasized that animal breeding estimates variances from individuals while plant breeding estimates variances from progeny families. Lush's (1945) definition of heritability is accurate but heritability has been estimated using various methods which sometimes do not appropriately consider the relationship of the type of progeny that are selected among (selection unit) with the type of progeny which the effects from selection are

expected (target response unit). Heritability in this definition ($\sigma_A^2 / \sigma_{Ph}^2$) is only appropriate when applied to individuals or mass selection.

Comstock (1964) uses an extension of Lush's (1940) concept of heritability by estimating σ_A^2 as a function of total progeny family variance, σ_f^2. For example, only ¼ of the total genetic variance among half-sib progeny where the coefficient of inbreeding is zero is attributed to additive variance (Hallauer, 1988). By manipulating the family structure of progeny evaluated, Comstock (1964) emphasized that the genetic variance may be increased among progeny families and this increased variance may be exploited for genetic improvement. Because additive effects were thought to be of high importance, some assumptions were made in the derivation of the heritability term in the genetic gain equation. Due to these assumptions about the importance of additive effects, a covariance between the selection unit and the response unit was substituted with the additive variance in the heritability term. The critical argument was that by merely increasing the additive variance via family structure manipulation, heritability also was increased (Comstock, 1964). Comstock (1964) used the heritability term in this manner in a genetic gain equation and compared multiple recurrent selection methods. Based on these comparisons, Comstock (1964) proposed inbred progeny recurrent selection as the superior choice of breeding methods for maize improvement if additive effects were important for quantitative traits. Noteably, heritability may also be influenced by the method in which it is estimated. As various methods were implemented for estimation of heritability, Hanson (1963) argues adamantly that heritability estimates should not be published without methods for their estimation and inclusion of variance components. He calls attention to a "reference unit"

from which heritability is estimated as an individual plant, a sample of plants in a plot, several replications of plots at a particular environment, or multiple replications of plots at multiple environments. This point is made so that reduction of genetic variance via experimental design is not misinterpreted when comparing heritability. While the clarification for uniformity of a definition of heritability was presented, it still was not complete for the proper use in the genetic gain equation in all situations (Hanson, 1963).

Current Theory

Hanson (1963) also brings to our attention that the true heritability is determined by the covariance of the population from which progeny are selected (selection unit) with the population from which progeny are measured for response (response unit) divided by the variance among progeny of the selection unit. This concept is clearly outlined in a comprehensive review on heritability by Holland (2003). Nyquist (1991) through mathematical derivations reminds us that heritability for use in the genetic gain equation is a regression problem where the realized response equals $R = b_{YX}S$, where R is the genetic gain, b_{YX} is the regression coefficient, Y is the response unit, X is the selection unit, and S is the selection differential. b_{YX} by definition is the cov(X,Y)/var X (Steele et al., 1997). So in this sense, the numerator for heritability depends on the covariance between the selected progeny and the progeny in which the response is predicted. This concept forces the breeder to clearly define the type of progeny the breeder is trying to improve from the type of progeny being selected. Several selection schemes were presented by Fehr (1991) and the progeny developed for evaluation from the various schemes represent the selection unit. Many

response units exist, which have not always been clearly defined and are not as clear to conceive as the selection units. The response unit may be the selected progeny directly (i.e., remnant seed of the genotypes evaluated), selected progeny self pollinated to any level of inbreeding, the selected progeny intermated (forming a new population), or selected progeny intermated and self pollinated to any level of inbreeding (Holland, 2003). The most applicable response unit may be either of the latter as they are the product of recurrent selection (Hallauer, 1992). If definitions of heritability include the selection units and response units there no longer exists a need for assumptions of importance of additive effects because they are integral in the expression of the covariance parameters (Hanson, 1963; Nyquist, 1991; Holland, 2003).

Harris (1964) developed a regression model to estimate the covariance between inbred relatives. Three studies have used Harris' (1964) covariance model to estimate the covariance of inbred relatives in maize populations (Wardyn, 2006; Edwards and Lamkey, 2002; Coors, 1988). Coors (1988) decomposed a narrow based maize population under simultaneous half-sib - S_1 inbred progeny recurrent selection to determine if the simultaneous selection methods were warranted. Edwards and Lamkey (2002) decomposed the BS13(S)C0 maize population, a broad based population after eight cycles of half-sib selection. Wardyn (2006) decomposed the BSCB1(R)C13 maize population, a broad based population after thirteen cycles of reciprocal half-sib selection. D1 is the covariance between additive effects and inbred homozygous dominance deviations (Harris, 1964). When D1 is negative, selection of inbred progeny may not be effective for improvement of outbred individuals, however if positive the converse is true (Coors, 1988). All three studies estimated D1 as negative for grain yield (Wardyn, 2006; Edwards and Lamkey, 2002; Coors,

1988). Wardyn (2006) extended the variance components to the genetic gain equation for multiple selection units and multiple response units as defined by Holland (2003). Wardyn (2006) found that the population of non-inbred progeny had the highest predicted gain for half-sib selection method, whereas progeny self pollinated for two generations of selfing (S_2 progeny) had the highest predicted gain for S_2 inbred progeny recurrent selection. Though this might seem trivial, this contradicts predictions reported earlier (Cockerham and Matzinger, 1985; Comstock, 1964).

Realizing Response

According to the scientific method upon development of a hypothesis, it must be tested for rejection or lack of rejection. Several experiments were conducted in which to test the hypothesis that inbred progeny recurrent selection is superior to other selection methods that have been conducted (Comstock, 1964).

Jinhayon and Russell (1969) evaluated a Lancaster maize population after three cycles of S_1 recurrent selection as outlined by Jenkins (1940) selecting for progeny with superior resistance to *Diplodia zeae* upon artificial inoculation with the fungus in an attempt to develop a resistance to stalk lodging. Klenke et al. (1989) evaluated the BS9(CB) maize population (Russell and Guthrie, 1982) after four cycles of S_1 recurrent selection selecting progeny with superior resistance to insect tunneling from artificial infestation of European corn borer (*Ostinia nubilalsis*). Hoard and Crosbie (1985) evaluated five cycles of S_1 recurrent selection in two populations, BS13(SCT) and BSSS2(SCT) (Mock and Eberhart, 1972), selecting progeny with superior traits that influenced cold tolerance. Each of these three studies has outlined positive short-term responses from S_1 recurrent selection. These

findings however, do little more than prove that S_1 recurrent selection was effective for improving the traits of interest in these particular populations. Iglesias and Hallauer (1989) summarized data from BS2, BSTL, and BS16 maize populations after four or five cycles of S_2 progeny selection with yield as the primary selection criteria. For all three programs that Iglesias and Hallauer summarized, yield gains did not support inbred progeny selection as a viable selection method. Iglesias and Hallauer concluded that the frequency of fixation of alleles in an inbred progeny selection program is too rapid for small finite populations and larger effective population sizes may be helpful. Regardless of the cause of failure for S_2 progeny recurrent selection to be effective for grain yield in these three populations, little evidence is present which compares the inbred progeny selection method with other forms of selection.

To test the hypothesis that one selection method is superior to another, the two selection methods need to be conducted from the same base population under the two types of selection. Such experiments have been conducted. Horner et al. (1989), Horner (1983), and Horner et al. (1973) made direct comparisons of testcross selection and inbred progeny recurrent selection methods upon five, three, and four cycles of selection, respectively, from three different founding populations. The respective selection methods were all initiated upon formation of the founding populations in an attempt to make direct comparisons of the effectiveness of the corresponding recurrent selection methods. In each of the studies, grain yield was the primary trait selected. After five cycles of selection Horner et al. (1973) reported that S_2 progeny and testcross selection methods were equally effective for increasing yield in the populations per se and testcross methods were superior for the improvement of combining ability. The Horner (1983) study revealed that no selection method was superior

for population per se improvement or improvement of combining ability. Horner et al. (1989) concluded that the testcross selection method was superior for improvement of both combining ability and the population per se. All three studies reported that S_2 progeny recurrent selection was superior for improving the performance of inbred populations (bulk samples of S_1 and S_2 progeny). The conclusion for lack of superior responses from S_2 progeny selection in each case was attributed largely to the importance of overdominance.

Tanner and Smith (1987) conducted a similar comparison study by comparing half-sib and S_1 progeny recurrent selection for eight cycles of selection in the Krug Hi I maize population (Lonquist, 1949). Tanner and Smith (1987) separated the responses observed into two discrete classes, those observed for cycle 0 through 4 and those observed for cycles 4 through 8. They observed that the grain yield gains of the population per se from the inbred progeny selection method were superior for the early cycles of selection. But, neither selection method was superior for improvement of grain yield for the latter cycles of selection. Additionally, upon removal of effects from random genetic drift, yield gains for both selection methods were less than predicted. Tanner and Smith (1987) reported similarly to Horner et al. (1983), Horner (1983), and Horner et al. (1989) that S_1 progeny selection resulted in decreased inbreeding depression and produced better yielding bulk samples of S_1 progeny. In addition to non-additive gene action, Tanner and Smith (1987) attributed the inferior gain predictions to over-estimated heritabilities used in their prediction equations and a reduction in genetic variance in the population after multiple cycles of selection.

Previous Evaluations of BS13(S)

The development of the BS13(S)C0 population followed a lineage of seven cycles of selection via a half-sib recurrent selection in the Iowa Stiff Stalk Synthetic maize population (BSSS) and one cycle of selection for resistance to cold germination and European corn borer feeding (Lamkey, 1992). After screening BSSS(HT)C7 (where (x) designates the selection method and Cn designates the n^{th} cycle of selection) for cold tolerance and European Corn Borer damage it was renamed BS13(S)C0. Currently eleven cycles of S_2 progeny recurrent selection have been conducted in the BS13(S) maize population. The selection method in BSSS was changed from a half-sib recurrent selection method to a S_2 progeny recurrent selection method in an attempt to increase the realized gain from selection. "One of the ways to increase gain from selection is to increase the additive genetic variance among families under evaluation" (Eberhart, 1970). This would be achieved by evaluating S_2 progeny as the additive variance among progenies is increased by inbreeding progeny. The covariance among half-sib progeny is $\frac{1}{4}\sigma_A^2$, the covariance among S_1 progeny equals $\sigma_A^2 + 1/4\sigma_D^2$ Sprague and Eberhart, 1977), and the covariance among S_2 progeny equals $\frac{3}{2}\sigma_A^2 + \frac{3}{16}\sigma_D^2$ (Hallauer and Miranda, 1988). Sprague and Eberhart (1977) did indicate that unless dominance effects are negligible, the improvement in the population per se cannot be predicted exactly. If the dominance effects are not negligible then the predicted improvement should be expected in a random set of S_1 lines.

Studies presented should be adequate to reject the theory that S_1 and S_2 progeny recurrent selection methods are superior to other forms of recurrent selection methods.

Explanations for failure of these superior gain predictions have yet to be empirically tested however. The BS13(S) maize population has been evaluated twice for response to S_2 progeny selection. Helms et al. (1989) conducted a study including cycles C0, C2, and C4 of BS13(S). The focus of Helms et al. (1989) was to compare effects of genetic drift of three related maize populations including BS13(S). In so doing, if the effects from random genetic drift were significant, an explanation of the deviation of realized responses from the predicted responses might be explained (Falconer and MacKay, 1996; Smith, 1983). Helms et al. (1989) concluded that effects due to random genetic drift were the same for all three populations and was not responsible for changing the genetic parameters of the populations. Response from S_2 progeny selection in BS13(S) was effective for improvement of grain yield in the population per se with a response of 0.226 t ha^{-1}, which was not a superior method as the genetic gain theory at that time predicted, and this deviation from the prediction was not explained by random genetic drift.

Lamkey (1992) conducted a comprehensive study of the response of fifty years of selection in the closed breeding population of the Iowa Stiff Stalk Synthetic that included BS13(S). Because of the difference in population selection methods, response to selection were reported distinctly for the BSSS(HT) program and the BS13(S) program. The only response units evaluated were the populations per se. An average response per cycle of selection observed for the BSSS(HT) program in grain yield was 0.164 t ha^{-1}. The response per cycle of selection observed for the BS13(S) program in grain yield was 0.009 t ha^{-1}. The large discrepancy of grain yield responses between Lamkey (1992) and Helms et al. (1989) was due to the lack of improvement in cycles four, five, and six for grain yield causing a significant quadratic pattern of response. This evidence suggested that S_2 progeny recurrent

selection was not an effective method for long-term improvement in maize. Lamkey (1992) gives three reasons for possible lack of response of S_2 progeny recurrent selection in the BS13(S) population, including a lack of genetic variance, overdominant gene action, and random genetic drift. Holthaus and Lamkey (1995) reported no change in additive genetic variance and in fact an increase in dominance variance between cycle zero and cycle six of BS13(S) refuting that lack of genetic variance caused the lack of response. Because the coefficient of inbreeding (Falconer and MacKay, 1996) for BSSS(HT)C7 is 29% (Eberhart, 1973) and the response of the per se population is positive, important overdominant gene action is not likely. Random genetic drift likely plays a role in response from selection in all populations (Smith, 1983). Evidence for effects from random genetic drift in BS13(S) being greater than effects from random genetic drift in other populations under effective recurrent selection are not present (Helms et al., 1989). It is unlikely that random genetic drift is limiting response of the population per se in the BS13(S) population to the extent realized.

Reasons for the limited response of S_2 progeny recurrent selection may be relative to the current theory, based on an accurate definition of the heritability term used in the genetic gain equation. However empirical support has yet to be reported. The objective of this dissertation is to empirically support current genetic gain theory reported by Edwards and Lamkey (2002) and Wardyn et al. (in review).

The focus of this dissertation is to measure the realized responses of various response units from multiple cycles of the BS13(S) maize population. Specifically, average responses regressed across cycles of selection to remove random deviations of the population will be investigated along with specific patterns of response in each of the response units. In so doing support may be added to the development of the genetic gain equations reported by

Wardyn et al. (2006) giving the breeder better tools to aid in choosing truly superior selection methods for germplasm with similar genetic population parameters as those investigated here.

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CHAPTER 3. RESPONSE TO SIX CYCLES OF S_2 PROGENY RECURRENT SELECTION IN THE BS13(S) MAIZE POPULATION

A paper to be submitted for publication in Crop Science

Clinton J. Turnbull, Jode W. Edwards*, and Kendall R. Lamkey

Introduction

"One of the ways to increase gain from selection is to increase the additive genetic variance among families under evaluation" (Eberhart, 1970). Based on this presumption, increasing genetic gain from selection should be achieved by evaluating S_2 progeny as the additive genetic variance among progenies is increased by inbreeding. Genetic variance is a fixed population genetic parameter which is partitioned into within progeny families and among progeny families. When considering only additive and dominance covariances, the covariance among half-sib progeny equals $\frac{1}{4}\sigma_A^2$, the covariance among S_1 progeny equals $\sigma_A^2 + 1/4\sigma_D^2$ (Sprague and Eberhart, 1977), and the covariance among S_2 progeny equals $\frac{3}{2}\sigma_A^2 + \frac{3}{16}\sigma_D^2$ (Hallauer and Miranda, 1988). The additive variance among inbred progeny is greater than among non-inbred progeny.

Multiple investigations of quantitative genetics were launched to answer the question of gene action in maize (Gardner, 1963; Moll et al., 1964; Moll and Robinson, 1967; Eberhart et al., 1966). The studies supported dominance as the most important form of gene action. Overdominance did not appear as important as dominance (Sprague and Eberhart,

1977 p. 326). Additionally, additive variance accounted for the largest portion of gene action in maize populations (Eberhart et al., 1966); but of the non-additive portion of gene action, dominance seems to predominate overdominance. The findings of dominance being the leading cause of gene action and additive effects accounting for most of the variation among progeny were evidence that superior genotypes need not be hybrid cultivars. The importance of additive effects led to the conclusion that inbred progeny recurrent selection should be superior to other selection methods (Comstock, 1964).

S_1 and S_2 progeny recurrent selection are both inbred progeny recurrent selection methods that have been evaluated extensively (Horner et al., 1989; Iglesias and Hallauer, 1989; Tanner and Smith, 1987; Klenke et al., 1986; Hoard and Crosbie, 1985; Horner, 1983; Horner et al., 1973; Jinahyon and Russell, 1969). While some of the evaluation studies report positive responses for disease resistance (Jinahyon and Russell, 1969), insect resistance (Klenke et al., 1986), or cold tolerance (Hoard and Crosbie, 1985), none have proven inbred progeny recurrent selection as superior to other methods of recurrent selection for long term response of grain yield.

Previously breeders have made assumptions about the importance of dominance variance being small relative to additive variance (Eberhart, 1966). If no assumptions about gene action are made, the exact response to selection must be developed with the covariance between the selection unit and the target response unit (Wardyn, 2006; Hanson, 1963). Edwards and Lamkey (2002) have estimated five genotypic covariance components for the BS13(S)C0 maize population.

The objective of this study is to determine how effective S_2 inbred progeny recurrent selection is for improving grain yield. To determine the effectiveness of S_2 inbred progeny

recurrent selection, this evaluation study will estimate the response of BS13(S) to six cycles of S_2 progeny recurrent selection in four types of response units including the response of the panmictic response unit [(often referred to as the population per se and/or target response unit of BS13(S)], a population of unrelated progeny with an inbreeding level equal to that of a population at $F_{IS} = 0.5$ (often referred to as the S_1 response unit), a population of unrelated progeny with an inbreeding level equal to that of a population at $F_{IS} = 0.75$ (often referred to as the S_2 response unit), and outbred response units. This study will estimate the average response per cycle of selection as well as the realized heritability for multiple agronomic traits. The null hypothesis for each response unit is that the average response per cycle of selection equals zero. Another test for effectiveness of S_2 inbred progeny recurrent selection is to test the null hypothesis that the realized heritabity for each of the response units is zero.

Materials and Methods

Genetic Materials and Selection Procedures

The Iowa Stiff Stalk Synthetic maize population (BSSS) was formed in 1939 by intermating 16 inbred lines (Sprague, 1946). The 16 inbred lines included in BSSS were chosen based on superior stalk qualities as determined by screening evaluations conducted by maize breeders across the U. S. cornbelt in 1933 and 1934. Half-sib (HT) recurrent selection was conducted in BSSS for seven cycles using a double-cross hybrid, Iowa 13 [(L317 *x* BL349) *x* (BL345 *x* MC401)], as the tester. After screening BSSS(HT)C7 [where BSSS designates the progenitor population, (HT) designates the selection method and C7 designates the 7^{th} cycle of selection] for cold tolerance and European Corn Borer damage it was renamed BS13(S)C0. As additive effects were thought to be of greater importance than

non-additive gene effects an inbred progeny selection program was implemented (Eberhart, 1970). Inbred progeny selection (S_2 progeny recurrent selection) was initiated in the BS13(S)C0 maize population in 1970 by the Cooperative Federal-State maize breeding program at Iowa State University (Lamkey, 1992). The first year of evaluation of S_2 progeny from BS13(S) was in 1972 and the formation of BS13(S)C6 was in the 1986-1987 winter nursery.

The primary trait under selection was always grain yield in the BS13(S) program. Throughout the history of the program however, some inconsistencies occurred. The selection unit was not always S_2 progeny and the recombination unit varied between S_1 and S_2 progeny. Selection intensities and selection differentials varied as well. Though the primary trait selected has always been grain yield, various techniques have been implemented to make the selections. Cycles 0 through 2 used no formal selection index though selection pressure for low grain moisture and reduced plant lodging at harvest was conducted in conjunction with selection for high grain yield. Selection of progeny from cycle 3 used a formal selection index though definitions are unavailable (Smith and Guy, 1981). Cycles 4 and 5 utilized a formal heritability selection index including selection for high grain yield, low grain moisture, low root lodging, and low stalk lodging. In this index each trait is weighted by its corresponding heritability. Cycle six utilized a multiplicative index with the same traits selected as in the heritability index. Development of the BS13(S) population for cycle 0 through cycle 6 has been summarized in Tables 3.1 and 3.2. A more detailed description of population development is available (Lamkey, 1992).

Experimental Procedures and Data Collection

Four types of response units were evaluated in this study 1) populations of unrelated individuals with an expected average inbreeding level in relation to the base population of F_{IS} = 0 (Wright, 1984), 2) outbred populations, 3) populations of unrelated individuals with an expected average inbreeding level in relation to the base population of F_{IS} = 0.5 (Wright, 1984), 4) and populations of unrelated individuals with an expected average inbred level in relation to the base population of F_{IS} = 0.75 (Wright, 1984). F_{IS} = 0, F_{IS} = 0.5 and F_{IS} = 0.75 in the literature are sometimes referred to as S_0 or panmictic, S_1, and S_2 populations, respectively.

The F_{IS} = 0 response units were developed from intermating all combinations of superior individuals from the BS13(S)C_{n-1} population via the bulk entry diallel method (Fehr, 1991 p. 147) followed by random mating bulk diallel progeny. The outbred response units were developed from a random sample of progeny from the F_{IS} = 0 population cross pollinated with five different testers. The five testers were BSSS, BS26 (Hallauer, 1986), Mo17 (Zuber, 1973), B91 (Russell, 1989), and BS13(S)C0. The response unit at F_{IS} = 0.5 was developed from self pollinating a random sample of unrelated individuals from the panmictic population for one generation. The response unit at F_{IS} = 0.75 were developed from self pollinating a random sample of unrelated individuals from the panmictic population for two generations. Grain harvested from each of the respective response units was represented in bulk samples.

This study was composed of three separate experiments. The first experiment consisted of treatments from the F_{IS} = 0 response units and outbred response units and will be referred to as the non-inbred experiment. The second experiment consisted of treatments

from the $F_{IS} = 0.5$ response units and will be referred to as the $F_{0.5}$ experiment. The third experiment consisted of treatments from $F_{IS} = 0.75$ response units and will be referred to as the $F_{0.75}$ experiment. Because plant vigor is reduced with selfing (Shull, 1908) it was important to separate treatments into these three separate experiments to minimize plant competition between treatments of varying levels of selfing.

The three experiments contained material from eight source populations, BS13(S)C0, cycles one through six of the S_2 progeny recurrent selection program (BS13(S)C1, BS13(S)C2, BS13(S)C3, BS13(S)C4, BS13(S)C5, and BS13(S)C6) and BSSS. The treatments in the non-inbred experiment included eight panmictic response units and 40 outbred response units all derived from the eight source populations. The panmictc response units were each included twice in the treatment design. Additionally the BS26 panmictic population and the population cross BSSS(R)C11 x BSCB1(R)C11 were used as checks in this experiment. The treatments in the $F_{0.5}$ and $F_{0.75}$ experiments included the same eight source populations as the non-inbred experiment.

All experiments were evaluated in 1991 at four Iowa locations (Ames Agronomy Farm, Ames Atomic Energy Farm, Ankeny, and Conrad) and in 1992 at four Iowa locations (Ames, Ankeny, Crawfordsville, and Martinsburg). Three replications per location were grown in the non-inbred experiment while five replications per location were grown in the $F_{0.5}$ and $F_{0.75}$ experiments. Experiments were grown in randomized complete block designs at each environment. Due to poor stands at Conrad in 1991 and Crawfordsville in 1992 only two replications of data in the non-inbred experiment were taken for these locations. Data were only included in the analysis for three replications of the $F_{0.5}$ and $F_{0.75}$ experiments at Conrad in 1991 for the same reason.

Experimental units for agronomic evaluations were two row field plot 5.47 m long with 0.76 m between rows. All plots were overplanted and thinned to uniform stands of ≈ 68,820 plants ha^{-1} at Conrad and ≈ 62,140 plants ha^{-1} at all other locations. All plots were machine planted and machine harvested. Data for grain yield (t ha^{-1}), grain moisture (g kg^{-1}), and root lodging (percentage of plants inclined more than 30 ° from vertical) were collected from eight environments. Data for stalk lodging (percentage of plants broken at or below the ear node) were taken from seven environments. Data for 50% silk emergence and 50% pollen shed (days after planting) were taken at the Ames Agronomy Farm in 1991. Ear height (cm) and plant height (cm) were taken from three environments in 1991. Ear and plant heights were calculated as the average of measurements for 10 competitive plants per plot and measured as the distance from the soil surface to the highest ear-bearing node (ear height) and the node of the flag leaf (plant height).

Statistical Methods

Transforming Data

Because of the use of a heritability selection index as selection criteria in some of the cycles of BS13(S) (Table 3.2), the change in the value of the index across cycles of selection may be considered a direct response to selection. For an exact response of the heritability index, it can only be appropriately measured in the population at $F_{IS} = 0.75$ because heritability varies with the level of inbreeding (Holland et al., 2003). Because the heritability index was not used in all cycles of selection the exact index is unattainable, however the following index was developed to approximate the response of the heritability selection index

when it was used as a selection criteria (Table 3.2):

$$Index = \frac{h^2_{yield}}{h^2_{yield}} * (yield) - \frac{h^2_{moisture}}{h^2_{yield}} * (moisture) - \frac{h^2_{rootlodging}}{h^2_{yield}} * (rootlodging) - \frac{h^2_{stalklodging}}{h^2_{yield}} * (stalklodging)$$

which we refer to as an average-index. The observed data from the current study were transformed with this index to assimilate selection pressure in relation to grain yield and analyzed similarly to the other agronomic traits. The observed repeatabilites from the evaluated S_2 progeny at each of the cycles during formation of the population (Table 3.2) were averaged for each of the traits involved in the selection index. Once the repeatabilites were averaged, a ratio of the repeatability of the selected trait to the repeatability of grain yield was used to obtain coefficients for each of the selected traits in the response units estimated in this study. When selecting multiple traits, the response for any one trait is reduced to $1/\sqrt{n}$ times as great as the response may have been if selection was exclusive for the trait of interest, where n is the number of traits selected (Bernardo, 2002). For this reason the average-index was developed to give a sense of efficiency of direct response. This is a similar concept to the use of the heritability index invoked during development of the population (weighting the traits with corresponding repeatabilities) however, due to the lack of use of the heritability index in every cycle of advancement true selection index coeffecients are unattainable and our averaged-index is a valid substitute for approximating direct responses in the populations at $F_{IS} = 0.75$.

Analysis of the Data

A linear additive model including replications and treatments as fixed effects was developed for individual environment (year-location combination) analysis. Each of the

three experiments was analyzed separately for individual environments, blocking on replications. Predictions of individual observations from the linear additive model were used to check individual observations for outliers via the Anscombe-Tukey test for outliers (Anscombe and Tukey, 1963). Caution was used in removing data from the dataset by only removing clearly detected outliers with plausible explanations.

Once the individual environmental data was checked for outliers a linear additive model was developed to calculate treatment means across replications and environments and corresponding standard errors within each of the three experiments (non-inbred, $F_{0.5}$, and $F_{0.75}$ experiments). Environment, replications nested within environments, and treatments were the main effects and considered as fixed effects. The treatment X environment interaction was considered a random effect and was used as the treatment X environment variance to calculate appropriate standard errors for treatment means. Treatment means were adjusted for the environmental and replication effects according to standard least squares mean procedures (Steel et al., 1997). The standard errors of the means were calculated for the treatments as follows: $s_{\bar{Y}} = \sqrt{\frac{\sigma^2}{n}}$. The standard error of the mean varies accordingly to the unbalance of the data (unequal representation of treatments of the F_{IS} =0 response units and removal of some replicates of data in Conrad and Crawfordsville).

A model was developed to estimate the response to selection in each of the eight response units. To do this, a mixed model was developed which includes an effect to deal with the true common intercept of the panmictic and BS13(S)C0 outbred response units. The main effects of this model were: environment, replication nested within environment, intercept, treatment nested within tester, and cycle nested within tester. All main effects

except treatment were treated as fixed effects. The treatments, intercept X environment, and cycle X environment were considered random effects. The treatment was considered a random effect to account for the random deviations of the population from the regression due to random genetic effects found in the various cycles of BS13(S). Cycle nested within tester was included as a covariate to estimate the response to selection within each response unit as appropriate. Tests for quadratic and cubic responses were conducted by including appropriate higher order levels of cycle in the model. Testing for significant effects from the covariate used only the variance (cycle X environment variance) calculated within the corresponding response unit as the error term. The BS13(S)C0 intercept (b_0) and average responses per cycle (b_1) are reported with corresponding standard errors (Tables 3.3 and 3.4) calculated from this model with higher order polynomials indicated when they were significant. Tests for lack of fit were not possible due to the complexity of the model however.

A similar mixed model was developed to estimate response to selection effort, substituting the cycle of selection with the cumulative selection differential. The selection differential is the mean of the progeny evaluated subtracted from the mean of the progeny selected at each cycle of selection. The cumulative selection differential is the sum of the prior selection differentials ($Cn + Cn\text{-}1 + \ldots + Cn\text{-}n$). Regressing the treatment means on cumulative selection differentials gives a direct interpretation of response observed to the amount of effort used in the formation of the cycles of the population (Hanson, 1963). The average response of this regression is the realized heritability (h^2) from selection (Table 3.5).

Results

The averages for grain yield across environments were highest in the non-inbred experiment, followed by the $F_{0.5}$ and $F_{0.75}$ experiments, respectively, as expected. The mean grain yield of the BSSS, BS26, and BSSS(R)C11 x BSCB1(R)C11 checks, were 4.07 t ha^{-1}, 5.35 t ha^{-1}, and 7.77 t ha^{-1} respectively. The grain yield of the response units are reported in Table 3.3. Grain yield of the F_{IS} = 0 response unit did not respond to inbred progeny selection (Table 3.3). The grain yield intercept for BS13(S)C0 from the covariate model was 5.12 t ha^{-1} and the prediction for BS13(S)C6 was 5.27 t ha^{-1}. Grain yield responded favorably for the BS13(S)Cn X BS13(S)C0 outbred response unit, F_{IS} = 0.5 response unit, and F_{IS} = 0.75 response unit with the greatest average response over cycles of selection being in the F_{IS} = 0.5 response unit (Table 3.3). The response per unit effort (realized h^2) was favorable for grain yield in the F_{IS} = 0.5 response unit, and F_{IS} =0.75 response unit with the greatest realized h^2 in the F_{IS} = 0.5 (Table 3.5).

The average-index for F_{IS} = 0.5 and F_{IS} = 0.75 response units responded quadratically and linearly across cycles of selection, respectively (Table 3.4). The grain yield across cycles of selection for the B13(S)Cn X BS13(S)C0 outbred and the F_{IS} = 0.75 response units responded linearly, while the grain yield across cycles of selection for the F_{IS} = 0.5 response unit responded quadratically (Table 3.3). Response of grain moisture was quadratic within the F_{IS} = 0 and F_{IS} = 0.75 response units across cycles of selection (Table 3.3). A linear negative response was found for root lodging within the BS13(S)Cn X BS26 outbred and F_{IS} = 0 response units (Table 3.4). Stalk lodging revealed a quadratic response across cycles of selection within F_{IS} = 0.5 and F_{IS} = 0.75 response units and cubically in the F_{IS} = 0 response

unit (Table 3.4). A positive linear response pattern for pollen date was found in the $F_{IS} = 0$ response unit.

The realized h^2 was significant for grain yield in the $F_{IS} = 0.5$ and $F_{IS} = 0.75$ response units. Realized h^2 for root lodging was significant in the $F_{IS} = 0$ and $F_{IS} = 0.5$ response units. And realized h^2 for stalk lodging was significant in the $F_{IS} = 0.75$ response unit. Trait responses across cycles of selection with corresponding tests of significance and realized heritabilities have been summarized (Tables 3.3 – 3.5 and Figures 3.1 and 3.2).

Discussion

The BS13(S) population is an improved population having BSSS as its progenitor population. BSSS underwent seven cycles of half-sib recurrent selection followed by screenings for reduced European corn-borer feeding and superior cold germination and recombination before being renamed BS13. Grain yield gains for $F_{IS} = 0$ response units have been reported in previous studies for BSSS under half-sib recurrent selection with average rates of response per cycle being 0.164 t ha^{-1}, 0.074 t ha^{-1}, and 0.344 t ha^{-1} across seven cycles of selection (Lamkey, 1992; Helms et al., 1989; and Eberhart et al., 1973). Grain yield gains for $F_{IS} = 0$ response units have been reported in previous studies for BS13(S) with average rates of response per cycle across four and six cycles of improvement of 0.226 t ha^{-1} and 0.009 t ha^{-1} respectively (Lamkey, 1992 and Helms et al., 1989) compared to a response of 0.024 t ha^{-1} in our study (Table 3.3). Though linear regression coefficients are inconsistent between studies, it appears that the grain yield for the $F_{IS} = 0$ response unit of S_2 progeny recurrent selection is neither superior to half-sib recurrent selection in these related populations nor effective for improving grain yield.

To answer the primary question, "How has BS13(S) responded to inbred progeny recurrent selection?", multiple response units were defined. They include the $F_{IS} = 0$ response unit as envisioned by Comstock (1964), outbred response units (testcrossing the panmictic population with Mo17, B91, BS26, and BSSS), the panmictic population testcrossed to BS13(S)C0, the population at $F_{IS} = 0.5$, and the population at $F_{IS} = 0.75$.

The response of grain yield in the panmictic population to six cycles of selection indicates that inbred progeny recurrent selection has been ineffective. It has, however, been effective for improving grain yield of the $F_{IS} = 0.5$, $F_{IS} = 0.75$, and outbred BS13(S)Cn X BS13(S)C0 response units. The quadratic response for grain yield in the $F_{IS} = 0.5$ response unit may be partially attributed to the inconsistency of the selection units and recombination units throughout the history of the BS13(S) program (Table 3.1). The average grain yield response (0.10 t ha^{-1} $cycle^{-1}$) and realized heritability (0.08) in the $F_{IS} = 0.75$ response unit reveals a strong direct response to S_2 inbred progeny selection in this population. Though the grain yield average responses for $F_{IS} = 0$, $F_{IS} = 0.5$, and $F_{IS} = 0.75$ response units are not all statistically significant nor can they be statistically tested, their comparisons are warranted. These three response units for grain yield are 0.02 t ha^{-1} $cycle^{-1}$ for the $F_{IS} = 0$ response unit, 0.14 t ha^{-1} $cycle^{-1}$ for the $F_{IS} = 0.5$ response unit, and 0.10 t ha^{-1} $cycle^{-1}$ for the $F_{IS} = 0.75$ response unit. It appears that, if the projection the average responses remain constant through continued selection, the performance of the inbred response units may exceed that of the $F_{IS} = 0$ response unit (i.e. the inbred populations may outperform the population per se in BS13(S)). One must however be careful in making this assumption because the reason for the quadratic response of grain yield in the $F_{IS} = 0.5$ is unknown and this trend may also appear in latter cycles for the $F_{IS} = 0.75$ response unit. It seems that predictions in grain yield

performance of inbred populations upon successive cycles of selection equalling that of the panmictic population may be more conservative.

The linear response of the BS13(S)Cn X BS13(S)C0 outbred population supports the idea of accumulation of alleles in the BS13(S) acting favorably with those in BS13(S)C0 with average frequencies of the favorable alleles controlling yield being less than 0.5 in BS13(S)C0 (Eberhart, 1970). The population, in relation to allelic frequencies, is diverging from the base population at incremental rates across cycles of selection.

Selection for grain moisture has been ineffective for all response units. The quadratic response of grain moisture over cycles of selection in the $F_{IS} = 0$ response unit and the $F_{IS} = 0.75$ response unit and lack of response in the $F_{IS} = 0.5$ response unit is likely due to inconsistent selection pressure as indicated by the cumulative selection differential for grain moisture (Fig. 3). Effective selection for this trait is critically dependent upon timing of grain harvest. Inbred progeny recurrent selection has been effective for decreasing root and stalk lodging in the $F_{IS} = 0$ response unit but has not significantly affected the inbred response units. Root lodging decreased linearly on average 0.93% cycle^{-1} in the $F_{IS} = 0$ response unit. Stalk lodging responded cubically with an initial increase (BS13(S)C0-BS13(S)C2) followed by a decrease to BS13(S)C5 in the $F_{IS} = 0$ response unit. Selection pressure for stalk lodging has been inconsistent and in the undesired direction at times; interestingly the panmictic population has mimicked this pattern (Fig. 3). The response patterns in the $F_{IS} = 0$ response unit for root and stalk lodging compared to the pattern of selection pressure are strong evidence that selection in inbred selection units for these traits are effective for responses in the $F_{IS} = 0$ response unit and likely a strong inbred-outbred correlation exists. Lack of significant response in the inbred populations for root lodging

across cycles of selection is an artifact of the already low levels of root lodging and not reason to believe that selection is ineffective in these response units.

A direct response to the heritability selection index is measured via the average-index in the population at $F_{IS} = 0.75$. It is positive and linear at a rate of 24.57 percent cycle^{-1} indicating that the correlation of the heritability index of S_2 progeny and the average-index of a population at that same inbreeding level is high. As seen with the exceptional response of the average-index, it is effective in increasing the heritability selection index in the population at $F_{IS} = 0.75$.

The effectiveness of an inbred progeny recurrent selection program towards improving the panmictic population when other than additive effects are important for controlling gene action is dependent on the correlation of inbred and outbred individuals for the traits of interest (Hanson, 1963). Sprague and Eberhart (1977) did realize that the genetic gain equation (Comstock, 1964) would not be exact for prediction of the panmictic population for inbred progeny selection if dominance and epistatic variance was important, but they dismissed them as negligible and assumed the panmictic population response would parallel that of the population selection unit response. Furthermore, Hallauer and Miranda (1988) published methods for estimating a bias to be used in the numerator of the heritability estimate. Hallauer and Miranda (1988), however, determined that the bias estimate was too complex to estimate for standard selection programs and likely negligible.

When defining the narrow sense heritability to be used to calculate the genetic gain equation, a function of this correlation is appropriate, $h^2 = \frac{\mathrm{cov}(G, A)}{\sigma^2_{family}}$, where G is the genotypic value and A is the breeding value. In an outbred population, $\mathrm{cov}(G, A) = \sigma^2_A$,

however in a population at $F_{IS} = 0.75$, $\text{cov}(G, A) = \frac{3}{2}\sigma_A^2 + \frac{5}{4}D_1$, where σ_A^2 is the additive variance and D_1 is the covariance between additive and dominance effects in inbred individuals as defined by Harris (1964). The genetic gain equation outlined by Comstock (1964) and the gain equation derived from Harris' model (Wardyn, in review) are identical for a half-sib selection program. However the comparison of Comstock's model and that derived from Harris's model are not identical for inbred progeny recurrent selection when other than additive effects are important (Holland, 2003; Hanson, 1963). The magnitude to which the outcomes differ depends on the magnitude of D_1. To give a general idea of importance of these genetic parameters in BS13(S)C0, $\sigma_A^2 = 0.29$, $\sigma_D^2 = 0.32$, $\sigma_{S_2}^2 = 0.59$, and $D_1 = -0.18$ for grain yield ($Mg^2\ ha^{-2}$) (Edwards and Lamkey, 2002). Though genetic parameters vary from population to population and within populations from cycle to cycle (Hallauer, 1970 and Wardyn, 2006), in general D_1 appears to be large and negative. In the other two known populations with estimates of D_1 available; $D_1 = -0.38$ ($t\ ha^{-1}$) (Wardyn, 2006) and $D_1 = -309$ ($g\ plant^{-1}$) (Coors, 1988). Development of these genetic parameters for each cycle of selection may be developed only if individual inbred lines and their corresponding outbreds are evaluated simultaneously (Harris, 1964) and was not the scope of this study.

Conclusion

Because selection pressure for grain yield has been consistent across cycles of selection in the BS13(S) population (Fig. 3) and no significant response was detected in the panmictic response unit, the authors contend that S_2 progeny recurrent selection is ineffective for improvement of grain yield in the panmictic population. Multiple reasons exist that may cause failure of improvement from selection in a closed population such as BS13(S). Absence of genetic variance for grain yield would cause lack of improvement. However, Holthaus and Lamkey (1995) refute this cause and report that total genetic variance has changed little from cycle zero to cycle six and in fact the proportion of additive to dominance variance has slightly increased. Random genetic drift may influence response to selection in small finite populations. However if drift is affecting response, one expects the average response per cycle in the population per se to be greater than the average response per cycle of the testcross of various cycles to the base population (Smith, 1983), and is not the case here. Additionally Helms et al. (1989) dismiss random genetic drift as having greater effects in BS13(S) than other stiff stalk maize populations. Genotype-by-environmental interactions (g x e) are a valid concern in all selection programs which may slow improvement. If the environments in which progeny are evaluated [during the selection program] are too few or vary too greatly, larger g x e is expected for the various cycles and may erode gain from selection. However because progress has been made in many other programs at the Federal-State cooperative maize breeding program with similar experimental designs, we contend that g x e is not the primary cause for failure of response in the panmictic population, however it may have reduced expected gains in all response units. As stated by Comstock (1964) and Horner et al. (1969) overdominace would diminish expectations of genetic gain

from an inbred selection scheme. Evidence of overdominance-like gene action has been supported in this population (Edwards and Lamkey, 2002). Due to the limited response in the panmictic population of BS13(S) reported support may be added to psuedo-overdominance as the responsible gene action hypothesized (Edwards and Lamkey, 2002).

When D_1 is negative, favorable response from inbred progeny selection alone is not likely (Coors, 1988). We support the covariance parameters reported in Edwards and Lamkey (2002) for BS13(S)C0 from using the covariance model from Harris (1964) to completely define population parameters especially the largely negative D_1 coefficient because grain yield for the $F_{IS} = 0.5$ and $F_{IS} = 0.75$ response units have responded favorably while grain yield for the $F_{IS} = 0$ and outbred response units have not. From this study it appears that inbred (S_2)-outbred correlations are too low for adequate grain yield improvement while inbred-inbred (S_2-S_1 and S_2-S_2) correlations are high for grain yield. Stalk lodging and root lodging however, may have much stronger inbred (S_2)-outbred correlations than for grain yield as seen in the favorable response for root lodging across cycles of selection and as seen in the similarity of the panmictic population response pattern compared with the pattern of selection pressure for stalk lodging. Selection for grain moisture is ineffective in all response units likely due to inconsistent selection pressure.

Table 3.1. Summary of the selection units, recombination units, number of progeny recombined and evaluated, and selection intensity used in evaluating progeny of indicated cycles in the BS13(S) maize population.

Cycle of selection	Selection unit	Recombination unit	Number of progeny		Selection Intensity
			Recombined	Evaluated	
0	S_2	S_2	10	100	0.10
1	S_2	S_2	10	100	0.10
2	S_1	S_1	20	100	0.20
3	S_2	S_1	20	100	0.20
4	S_2	S_1	20	100	0.20
5	S_2	S_1	20	150	0.13
6	S_2	S_2	20	129	0.16

Table 3.2. Summary of the selection differentials, type of selection index, heritability, and year of progeny evaluation trials in the BS13(S) maize population.

		Selection Differential						Heritability				
Cycle of Selection	†Location of Progeny evaluations	Yield	Moisture	Root Lodging	Stalk Lodging	Index	Type of selection Index	Yield	Moisture	Root Lodging	Stalk Lodging	Year of progeny evaluation
		t ha^{-1}	g kg^{-1}	%	%			t ha^{-1}	g kg^{-1}	%	%	
0	Ames, Ankeny, Martinsburg	1.39	-8.0	-6.2	1.0	NA	None	0.81	0.87	0.49	0.18	1972
1	‡Ames, Ames, Martinsburg	1.75	2.0	-7.7	0.5	NA	None	0.67	0.87	0.69	0.43	1975
2	Ames, Ankeny, Martinsburg	1.03	2.0	0.5	2.5	NA	None	0.69	0.82	0.54	0.57	1978
3	Ames, Martinsburg, Columbia	1.12	-9.0	-0.1	-1.0	5.5	Unknown	0.51	0.66	0.24	0.33	1981
4	Ames, Ankeny, Martinsburg	0.64	-2.0	-4.3	-5.4	9.4	§Heritability	0.73	0.74	0.15	0.72	1984
5	Ames, Ankeny, Martinsburg	1.40	5.0	-1.9	-2.2	11.9	§Heritability	0.59	0.75	0.64	0.72	1987
6	Ames, Ankeny, Martinsburg	0.65	-4.0	-0.8	-5.5	149.6	¶Multiplicative	0.71	0.87	0.20	0.65	1990

†Ames, Ankeny, and Martinsburg are Iowa locations and Columbia is a Missouri location. Two replications evaluated at each location.

‡Two field locations near Ames; one at the agronomy farm and one at the atomic energy farm.

§A weighted summation index where the traits are weighted by their corresponding heritability.

¶A multiplicative index where the product of the selected traits is the index. In this case truncation values were assigned and the index = (Yield-30.6)*(Moisture-22.8)*(14.9-Root lodging)*(23.8-Stalk lodging).

Table 3.3. Summary of mean grain yields ± standard errors (se) for multiple response units of BSSS and BS13(S), least square linear regression intercept at BS13(S)C0, BS13(S) linear regression coefficients, and significance of linear, quadratic, and cubic effects. Linear regression coefficients were computed as the average change per cycle. 95% C. I. = se * $t_{0.025, d.f.}$; $t_{0.025, 5} = 2.571$.

	BSSS	BS13(S) Cycle of selection							†Regression coefficients for BS13(S)		
	C0	C0	C1	C2	C3	C4	C5	C6	b_0	b_1	*sig.*
	---t ha^{-1}---										
Testcrosses	Outbred response units										
Mo17	6.82 ± 0.26	8.20 ± 0.25	7.62 ± 0.24	6.95 ± 0.24	7.91 ± 0.24	8.34 ± 0.24	8.02 ± 0.25	8.14 ± 0.24	7.61	0.07 ± 0.06	
B91	6.66 ± 0.25	7.17 ± 0.25	7.39 ± 0.24	7.49 ± 0.25	7.24 ± 0.25	7.35 ± 0.24	7.57 ± 0.24	7.76 ± 0.24	7.20	0.07 ± 0.05	
BS26	5.84 ± 0.24	7.05 ± 0.24	7.42 ± 0.24	6.86 ± 0.24	7.28 ± 0.24	7.09 ± 0.24	7.32 ± 0.24	7.10 ± 0.25	7.10	0.01 ± 0.05	
BSSS	4.08 ± 0.24	5.71 ± 0.24	5.56 ± 0.24	5.49 ± 0.24	5.55 ± 0.24	5.75 ± 0.24	5.84 ± 0.24	5.88 ± 0.25	5.51	0.05 ± 0.05	
BS13(S)C0	5.71 ± 0.24	5.05 ± 0.21	5.51 ± 0.24	5.65 ± 0.24	5.61 ± 0.25	5.31 ± 0.24	5.53 ± 0.25	5.69 ± 0.24	5.12	0.09 ± 0.04	*l*
Per se	F_{IS} = 0 response units										
BS13(S)	4.08 ± 0.24	5.05 ± 0.21	5.02 ± 0.21	5.29 ± 0.21	5.33 ± 0.21	5.03 ± 0.21	5.30 ± 0.21	5.43 ± 0.21	5.12	0.02 ± 0.04	
	F_{IS} = 0.5 response units										
BS13(S)	2.97 ± 0.13	3.30 ± 0.13	4.09 ± 0.13	4.26 ± 0.14	4.27 ± 0.13	4.19 ± 0.13	4.40 ± 0.13	4.44 ± 0.13	3.73	0.14 ± 0.04	*q*
	F_{IS} = 0.75 response units										
BS13(S)	2.37 ± 0.13	3.40 ± 0.13	3.58 ± 0.14	3.55 ± 0.13	3.83 ± 0.14	4.08 ± 0.14	4.09 ± 0.14	3.79 ± 0.13	3.47	0.10 ± 0.04	*l*

l, *q* regression coefficients significant for linear and quadratic effects respectively at the 0.05 level of significance.

†Estimate of the linear regression coefficients when fitting only the linear effect in the model.

Table 3.4. Least squares linear response ± standard errors (se) to selection per cycle for eight agronomic traits after six cycles of S_2 progeny recurrent selection in the BS13(S) maize population. Linear regression coefficients were computed as the average change per cycle. 95% C. I. = se * $t_{0.025,\ d.f.}$; $t_{0.025,\ 5} = 2.571$.

	†Traits							
Populations	‡Index	Grain Moisture	Lodging		Height		Flowering Dates	
			Root	Stalk	Ear	Plant	Pollen	Silking
		g kg^{-1}	----------%----------		----------cm----------		---days after planting---	
Testcrosses				Outbred response units				
BS13(S) x Mo17	0.55 ± 0.63*c*	0.04 ± 0.11	0.22 ± 0.40	0.58 ± 0.32	-1.17 ± 0.63	-1.39 ± 0.90	0.10 ± 0.09*q*	-0.06 ± 0.06
BS13(S) x B91	0.76 ± 0.60	0.07 ± 0.10	-0.26 ± 0.31	-0.07± 0.28	0.08 ± 0.67	-0.05 ± 0.94	0.17 ± 0.11	0.05 ± 0.11
BS13(S) x BS26	0.67 ± 0.59	0.04 ± 0.09	-0.91± 0.40*l*	-0.01 ± 0.35	-1.12 ± 0.66	-0.59 ± 0.95*c*	0.05 ± 0.15	-0.07 ± 0.13
BS13(S) x BSSS	0.71 ± 0.63	-0.04 ± 0.09	-0.29 ± 0.39	-0.05 ± 0.31	-0.18 ± 0.72	0.38 ± 0.99	0.01 ± 0.10	-0.15 ± 0.08
BS13(S) x BS13(S)C0	0.77 ± 0.0.45	0.06 ± 0.07	-0.57 ± 0.37	-0.11 ± 0.23	-0.68 ± 0.49	-1.20 ± 0.81	0.29 ± 0.07	-0.48 ± 0.06*q*
Per se				F_{IS} = 0 response units				
BS13(S)	-0.01 ± 0.42	-0.02 ± 0.07q	-0.93 ± 0.33*l*	0.10 ± 0.22*c*	-1.51 ± 0.49*q*	-2.59 ± 0.69*l*	0.24 ± 0.07*l*	0.07 ± 0.06
				F_{IS} = 0.5 response units				
BS13(S)	1.53 ± 0.46*q*	0.06 ± 0.08	-0.50 ± 0.28	-0.03 ± 0.21*q*	0.32 ± 0.97	-0.37 ± 0.80	0.01 ± 0.07	0.00 ± 0.05
				F_{IS} = 0.75 response units				
BS13(S)	1.28 ± 0.46*l*	-0.04 ± 0.08*q*	-0.41 ± 0.30	-0.04 ± 0.21*q*	-1.27 ± 0.59*q*	-1.19 ± 0.84*q*	0.04 ± 0.09	-0.14 ± 0.08

l, q, c regression coefficients significant for the linear, quadratic, and cubic responses respectively at the 0.05 level of significance.

†Estimate of the linear regression coefficient when fitting only the linear effect in the model. ‡Proportional summation-index computed from an average of the heritabilities for the traits under selection, as computed in each of the years of advancement evaluation, proportionally to yield heritability multiplied by the observed values of the traits; *I = quintles – (h²moisture/h²quintles)*moisture – (h²root loginding/h²quintles)*root lodging – (h²stalk lodging/h²quintles)*stalk logding.*

Table 3.5. Summary of the realized heritabilities ± standard errors (se) for the four traits under selection in the BS13(S) maize population across six cycles of selection. The realized heritabilities were computed as the average change per unit of cumulative selection differential. 95% C. I. = se * $t_{0.025, d.f.}$; $t_{0.025,5} = 2.571$.

	Realized heritability		
Traits	$F_{IS} = 0$ response units	$F_{IS} = 0$ response units	$F_{IS} = 0$ response units
Grain Yield (t ha^{-1})	0.03 ± 0.03	0.12 ± 0.03**	0.08 ± 0.03**
Grain Moisture (g kg^{-1})	-0.34 ± 0.27	-0.06 ± 0.31	-0.34 ± 0.32
Root Lodging (%)	-0.31 ± 0.11**	-0.20 ± 0.08*	-0.12 ± 0.09
Stalk Lodging (%)	-0.28 ± 0.15	-0.17 ± 0.11	-0.25 ± 0.12*

*,** linear regression coefficient significant at the 0.05 and 0.01 level respectively

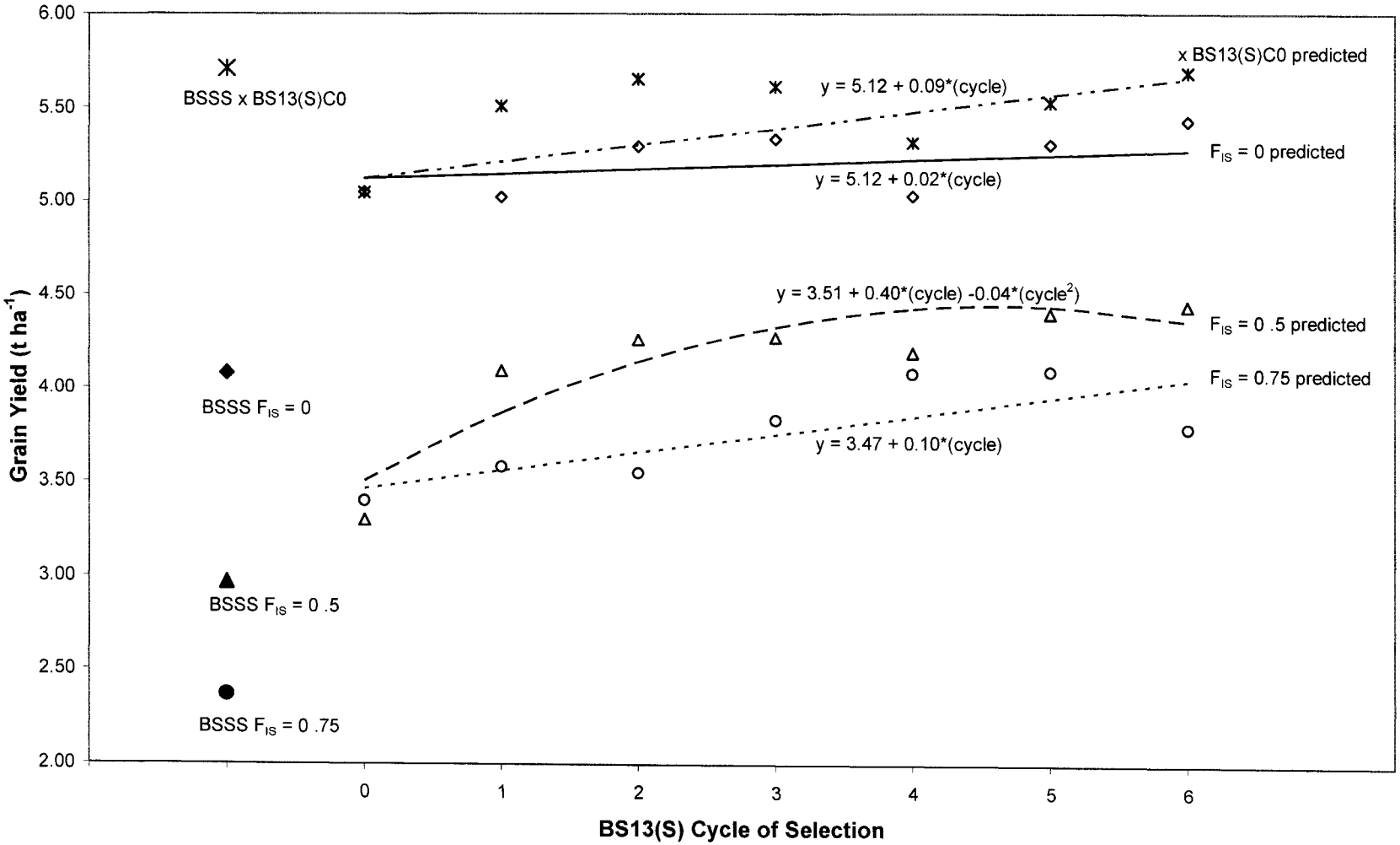

Figure 3.1. Observed values of BSSS and BS13(S) and predicted regressions of mean grain yields on six cycles of S_2 progeny recurrent selection in the BS13(S) maize population for $F_{IS} = 0$, $F_{IS} = 0.5$, $F_{IS} = 0.75$, and BS13(S) x BS13(S)C0 populations. Linear regression coefficients were significant for the BS13(S) x BS13(S)C0 and the $F_{IS} = 0.75$ populations. Quadratic regression coefficients were significant for the $F_{IS} = 0.5$ populations.

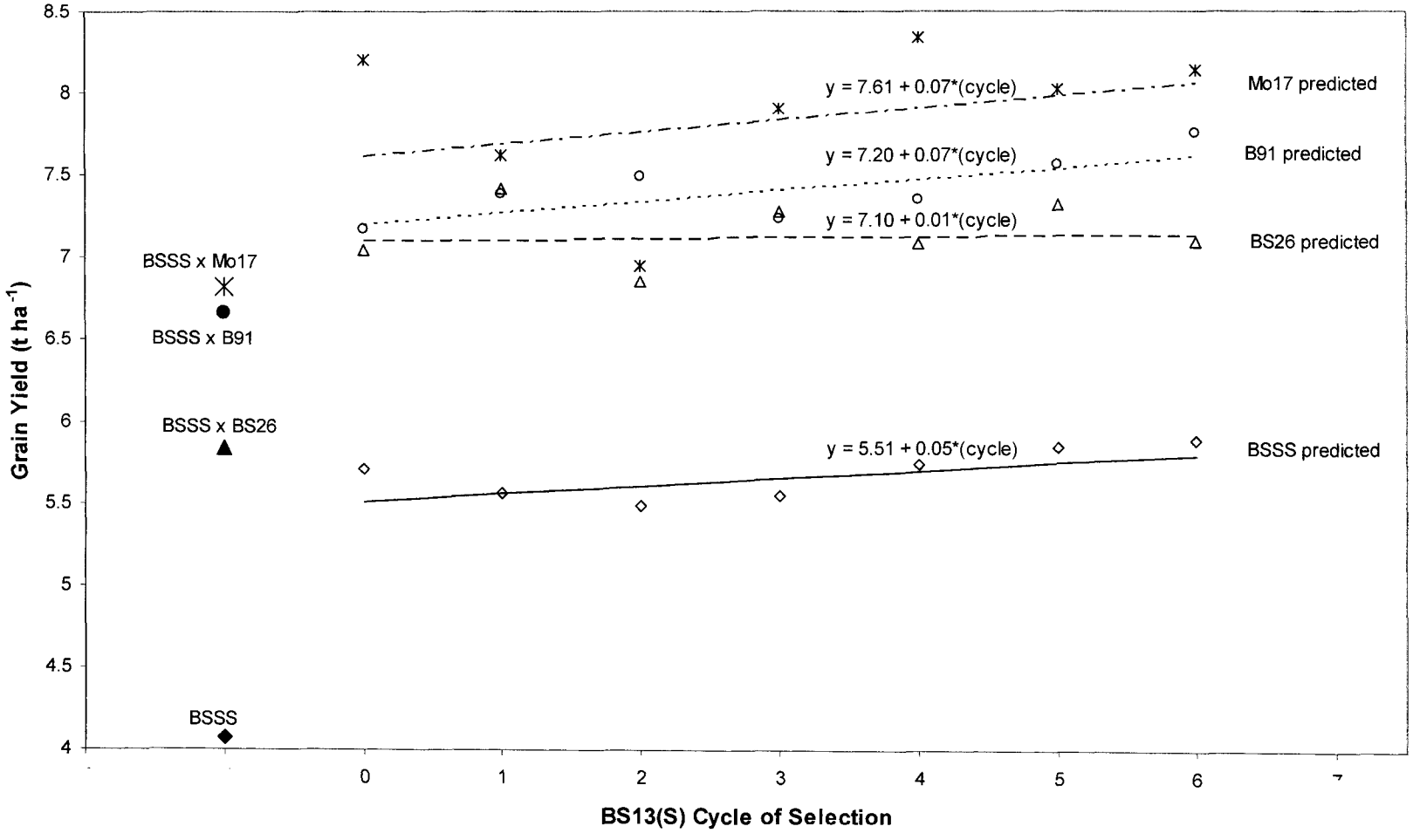

Figure 3.2. Observed values of BSSS and BS13(S) and predicted regressions of mean grain yields on six cycles of S_2 progeny recurrent selection in the BS13(S) maize population for testcrosses of BSSS, BS26, B91, and Mo17. The responses did not test significant for linearity or higher order polynomials.

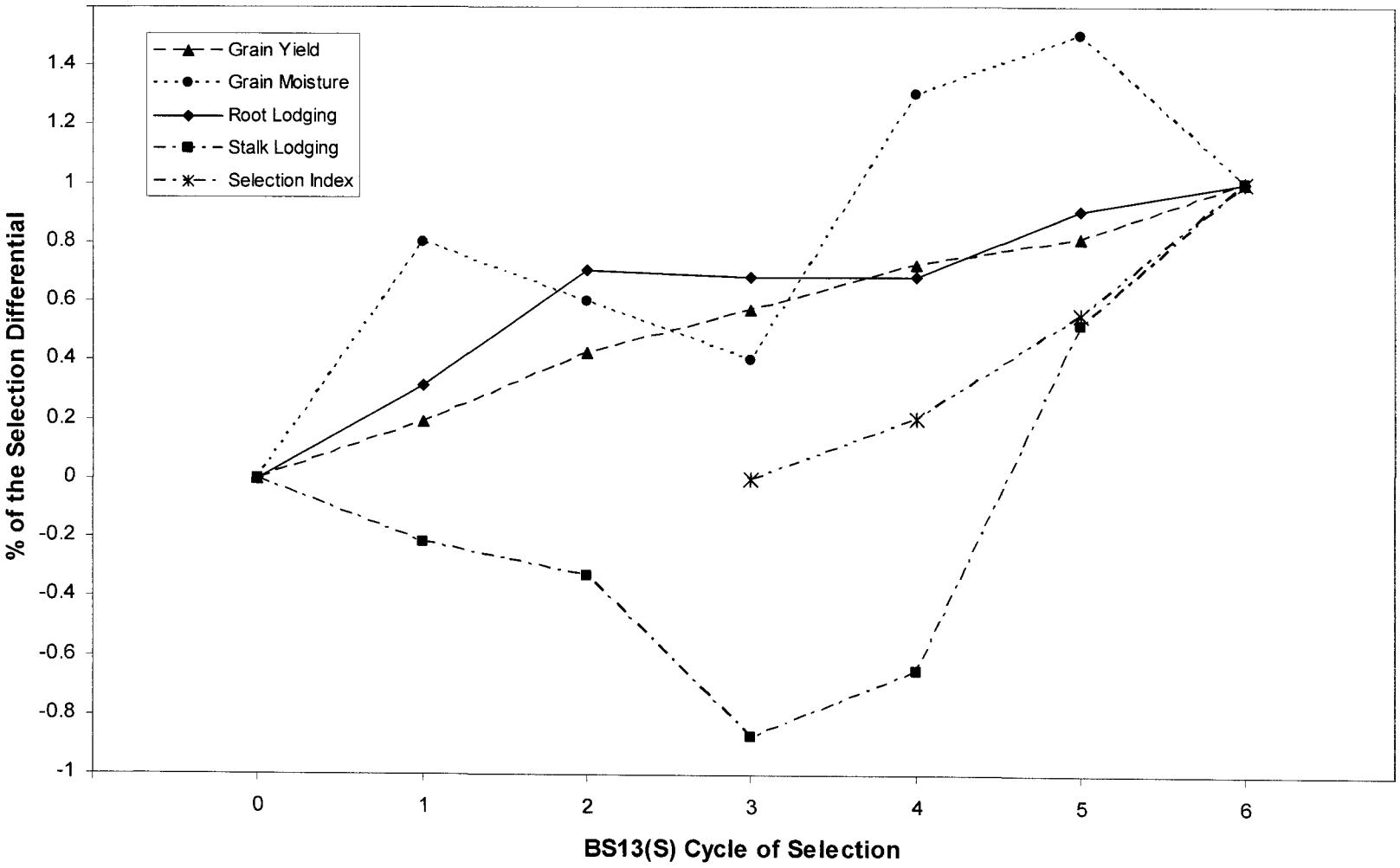

Figure 3.3. The cumulative selection differential for each trait under selection in BS13(S) maize population plotted at each cycle of selection on a percentage basis of cycle six.

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Appendix A. Supplemental Tables

Supplemental Table A.3.1. Summary of mean grain moisture ± standard errors (se) for multiple response units of BSSS and BS13(S), least square linear regression intercept at BS13(S)C0, BS13(S) linear regression coefficients, and significance of linear, quadratic, and cubic effects. Linear regression coefficients were computed as the average change per cycle. 95% C. I. = se * $t_{0.025,\ d.f.}$; $t_{0.025,\ 5} = 2.571$.

	BSSS	BS13(S) Cycle of selection							Regression coefficients for BS13(S)		
	C0	C0	C1	C2	C3	C4	C5	C6	b_0	b_1	*sig.*
	---------- g kg^{-1} ----------										
Testcrosses		Outbred response units									
Mo17	21.39 ± 0.43	21.00 ± 0.41	21.17 ± 0.41	20.00 ± 0.41	21.02 ± 0.41	20.02 ± 0.41	21.33 ± 0.41	21.20 ± 0.41	20.76	0.04 ± 0.22	
B91	19.77 ± 0.41	20.23 ± 0.42	20.6 ± 0.41	20.09 ± 0.41	19.63 ± 0.42	20.3 ± 0.41	20.86 ± 0.41	20.61 ± 0.41	20.21	0.07 ± 0.19	
BS26	21.77 ± 0.41	22.22 ± 0.41	21.18 ± 0.41	21.35 ± 0.41	22.70 ± 0.41	22.28 ± 0.41	21.64 ± 0.41	21.9 ± 0.42	21.89	0.04 ± 0.17	
BSSS	22.19 ± 0.41	22.16 ± 0.41	21.63 ± 0.41	21.50 ± 0.41	22.19 ± 0.41	21.45 ± 0.41	21.60 ± 0.41	21.90 ± 0.42	21.91	-0.04 ± 0.17	
BS13(S)C0	22.16 ± 0.41	22.10 ± 0.32	21.06 ± 0.41	21.81 ± 0.41	21.21 ± 0.42	21.36 ± 0.41	22.19 ± 0.42	21.59 ± 0.41	21.40	0.06 ± 0.15	
		F_{IS} = 0 response units									
Per se	22.19 ± 0.32	22.10 ± 0.32	20.60 ± 0.33	21.44 ± 0.32	20.69 ± 0.32	20.91 ± 0.32	21.13 ± 0.32	21.93 ± 0.32	22.70	-0.02 ± 0.14	*q*
		F_{IS} = 0.5 response units									
Per se	21.43 ± 0.20	20.67 ± 0.20	20.39 ± 0.20	20.63 ± 0.21	20.49 ± 0.20	20.29 ± 0.20	20.52 ± 0.21	21.30 ± 0.21	20.41	0.06 ± 0.16	
		F_{IS} = 0.75 response units									
Per se	21.27 ± 0.26	21.54 ± 0.26	20.92 ± 0.26	20.91 ± 0.25	20.63 ± 0.26	20.30 ± 0.26	21.04 ± 0.26	21.27 ± 0.26	22.40	-0.04 ± 0.16	*q*

q regression coefficients significant for quadratic effects at the 0.05 level of significance.

Supplemental Table A.3.2. Summary of mean root lodging ± standard errors (se) for multiple response units of BSSS and BS13(S), least square linear regression intercept at BS13(S)C0, BS13(S) linear regression coefficients, and significance of linear, quadratic, and cubic effects. Linear regression coefficients were computed as the average change per cycle. 95% C. I. = se * $t_{0.025,\ d.f.}$; $t_{0.025,\ 5} = 2.571$.

	BSSS	BS13(S) Cycle of selection							Regression coefficients for BS13(S)		
	C0	C0	C1	C2	C3	C4	C5	C6	b_0	b_l	*sig.*
	----------% root lodging----------										
Testcrosses		Outbred response units									
Mo17	4.33 ± 2.11	4.61 ± 2.04	3.16 ± 2.00	3.80 ± 2.00	2.89 ± 2.00	5.41 ± 2.00	6.86 ± 2.04	3.55 ± 2.00	3.58	0.22 ± 0.80	
B91	5.82 ± 2.00	8.53 ± 2.05	7.03 ± 2.00	7.46 ± 2.00	7.35 ± 2.05	5.70 ± 2.04	5.92 ± 2.00	7.33 ± 2.00	7.70	-0.26 ± 0.62	
BS26	10.82 ± 2.00	11.49 ± 2.00	11.18 ± 2.00	5.83 ± 2.00	6.43 ± 2.00	8.48 ± 2.04	5.51 ± 2.00	5.89 ± 2.05	10.40	-0.91± 0.80	/
BSSS	7.10 ± 1.58	8.00 ± 2.04	10.23 ± 2.00	7.78 ± 2.00	9.57 ± 2.00	7.58 ± 2.00	10.98 ± 2.04	4.85 ± 2.00	9.10	-0.29 ± 0.77	
BS13(S)C0	8.00 ± 2.00	12.41 ± 1.60	10.12 ± 2.00	11.31 ± 2.00	11.25 ± 2.14	9.53 ± 2.00	7.96 ± 2.05	10.91 ± 2.00	12.14	-0.57 ± 0.74	
		S_0 populations									
Per se	7.10 ± 1.58	12.41 ± 1.60	14.23 ± 1.61	8.05 ± 1.60	10.44 ± 1.62	8.01 ± 1.59	7.59 ± 1.62	7.45 ± 1.58	12.14	-0.93 ± 0.66	/
		S_1 populations									
Per se	7.22 ± 1.27	8.62 ± 1.28	7.65 ± 1.28	4.64 ± 1.29	6.14 ± 1.27	5.81 ± 1.27	4.89 ± 1.27	5.32 ± 1.28	7.62	-0.50 ± 0.55	
		S_2 populations									
Per se	4.75 ± 1.30	7.25 ± 1.30	7.40 ± 1.33	5.23 ± 1.27	7.28 ± 1.33	3.66 ± 1.30	6.75 ± 1.30	4.27 ± 1.29	7.15	-0.41 ± 0.60	

/regression coefficients significant for linear effects at the 0.05 level of significance.

Supplemental Table A.3.3. Summary of mean stalk lodging ± standard errors (se) for multiple response units of BSSS and BS13(S), least square linear regression intercept at BS13(S)C0, BS13(S) linear regression coefficients, and significance of linear, quadratic, and cubic effects. Linear regression coefficients were computed as the average change per cycle. 95% C. I. = se * $t_{0.025,\ d.f.}$; $t_{0.025,\ 5} = 2.571$.

	BSSS	BS13(S) Cycle of selection							Regression coefficients for BS13(S)		
	C0	C0	C1	C2	C3	C4	C5	C6	b_0	b_1	*sig.*
	----------% stalk lodging----------										
Testcrosses		Outbred response units									
Mo17	11.56 ± 1.75	5.68 ± 1.67	5.59 ± 1.64	6.05 ± 1.64	7.51 ± 1.64	10.20 ± 1.64	7.57 ± 1.67	8.3 ± 1.64	5.58	0.58 ± 0.64	
B91	6.51 ± 1.64	8.61 ± 1.68	7.00 ± 1.64	8.74 ± 1.64	8.95 ± 1.68	9.21 ± 1.67	7.62 ± 1.64	7.34 ± 1.64	8.57	-0.07± 0.56	
BS26	13.43 ± 1.64	10.41 ± 1.64	14.03 ± 1.64	13.23 ± 1.64	12.76 ± 1.64	14.15 ± 1.67	9.93 ± 1.64	12.59 ± 1.68	12.50	-0.01 ± 0.70	
BSSS	12.39 ± 1.36	8.87 ± 1.64	11.81 ± 1.64	10.68 ± 1.67	9.9 ± 1.64	12.57 ± 1.64	9.42 ± 1.64	9.27 ± 1.68	10.51	-0.05 ± 0.63	
BS13(S)C0	8.87 ± 1.64	6.48 ± 1.39	8.30 ± 1.64	8.00 ± 1.64	7.03 ± 1.75	7.46 ± 1.64	6.64 ± 1.68	8.78 ± 1.64	8.26	-0.11 ± 0.45	
		F_{IS} = 0 response units									
Per se	12.39 ± 1.36	6.48 ± 1.39	9.77 ± 1.39	10.09 ± 1.38	9.58 ± 1.40	9.07 ± 1.37	7.91 ± 1.39	7.84 ± 1.36	2.33	0.10 ± 0.45	*c*
		F_{IS} = 0.5 response units									
Per se	10.08 ± 0.69	5.31 ± 0.69	6.23 ± 0.70	6.19 ± 0.71	7.18 ± 0.69	5.95 ± 0.69	5.93 ± 0.69	5.14 ± 0.69	3.09	-0.03 ± 0.88	*q*
		F_{IS} = 0.75 response units									
Per se	7.21 ± 0.67	4.7 ± 0.67	5.73 ± 0.69	4.84 ± 0.66	6.65 ± 0.69	6.38 ± 0.67	4.74 ± 0.67	4.46 ± 0.67	2.35	-0.04 ± 0.42	*q*

q, *c* regression coefficients significant for quadratic and cubic effects respectively at the 0.05 level of significance.

Supplemental Table A.3.4. Summary of mean plant height ± standard errors (se) for multiple response units of BSSS and BS13(S), least square linear regression intercept at BS13(S)C0, BS13(S) linear regression coefficients, and significance of linear, quadratic, and cubic effects. Linear regression coefficients were computed as the average change per cycle. 95% C. I. = se * $t_{0.025,\ d.f.}$; $t_{0.025,\ 5}$ = 2.571.

	BSSS	BS13(S) Cycle of selection							Regression coefficients for BS13(S)		
	C0	C0	C1	C2	C3	C4	C5	C6	b_0	b_1	*sig.*
	cm										
Testcrosses		Outbred response units									
Mo17	184.9 ± 4.9	202.3 ± 4.2	197.2 ± 4.2	188.4 ± 4.2	196.7 ± 4.2	190.4 ± 4.2	191.8 ± 4.2	191.8 ± 4.2	200.3	-1.39 ± 1.90	
B91	201.9 ± 4.2	202.5 ± 4.5	197.7 ± 4.2	202.8 ± 4.2	201.8 ± 4.5	202.6 ± 4.2	203.2 ± 4.2	198.3 ± 4.2	203.5	-0.05 ± 2.00	
BS26	196.1 ± 4.2	203.6 ± 4.2	191.8 ± 4.2	187.8 ± 4.2	202.3 ± 4.2	197.6 ± 4.2	193.9 ± 4.2	193.8 ± 4.5	225.0	-0.59 ± 2.00	*c*
BSSS	183.9 ± 3.4	185.3 ± 4.2	179.9 ± 4.2	182.9 ± 4.2	184.7 ± 4.2	182.2 ± 4.2	183.6 ± 4.2	185.9 ± 4.5	184.6	0.38 ± 2.10	
BS13(S)C0	185.3 ± 4.2	183.4 ± 3.5	181.4 ± 4.2	179.2 ± 4.2	174.5 ± 4.5	176.9 ± 4.2	174.5 ± 4.5	166.7 ± 4.2	180.2	-1.20 ± 1.72	
		F_{IS} = 0 response units									
Per se	183.9 ± 3.4	183.4 ± 3.5	171.7 ± 3.6	166.7 ± 3.5	168.3 ± 3.6	168.0 ± 3.5	171.1 ± 3.5	162.8 ± 3.4	180.2	-2.59 ± 1.47	*l*
		F_{IS} = 0.5 response units									
Per se	166.6 ± 1.9	157.8 ± 1.9	164.3 ± 1.9	154.8 ± 2.0	161.3 ± 1.9	158.9 ± 1.9	158.1 ± 1.9	156.9 ± 2.0	159.5	-0.37 ± 1.69	
		F_{IS} = 0.75 response units									
Per se	155.5 ± 3.1	162.0 ± 3.1	152.9 ± 3.3	143.6 ± 2.9	147.2 ± 3.3	141.0 ± 3.1	156.5 ± 3.1	149.6 ± 3.0	165.0	-1.19 ± 1.77	*q*

l, q, c regression coefficients significant for linear, quadratic, and cubic effects respectively at the 0.05 level of significance.

Supplemental Table A.3.5. Summary of mean ear height ± standard errors (se) for multiple response units of BSSS and BS13(S), least square linear regression intercept at BS13(S)C0, BS13(S) linear regression coefficients, and significance of linear, quadratic, and cubic effects. Linear regression coefficients were computed as the average change per cycle. 95% C. I. = se * $t_{0.025, d.f.}$; $t_{0.025, 5} = 2.571$.

	BSSS	BS13(S) Cycle of selection							Regression coefficients for BS13(S)		
	C0	C0	C1	C2	C3	C4	C5	C6	b_0	b_1	*sig.*
	cm										
Testcrosses		Outbred response units									
Mo17	91.4 ± 2.9	103.4 ± 2.5	101.8 ± 2.5	95.9 ± 2.5	98.4 ± 2.5	97.6 ± 2.5	94.6 ± 2.5	96.7 ± 2.5	103.6	-1.17 ± 1.33	
B91	97.0 ± 2.5	98.5 ± 2.6	96.0 ± 2.5	98.5 ± 2.5	95.9 ± 2.6	98.2 ± 2.5	97.1 ± 2.5	98.9 ± 2.5	99.3	0.08 ± 1.42	
BS26	96.8 ± 2.5	107.6 ± 2.5	101.5 ± 2.5	94.7 ± 2.5	103.2 ± 2.5	99.9 ± 2.5	96.5 ± 2.5	98.8 ± 2.6	105.2	-1.12 ± 1.40	
BSSS	96.5 ± 2.0	97.5 ± 2.5	96.2 ± 2.5	93.9 ± 2.5	94.5 ± 2.5	96.1 ± 2.5	93.5 ± 2.5	96.7 ± 2.6	97.7	-0.18 ± 1.52	
BS13(S)C0	97.5 ± 2.5	95.6 ± 2.0	97.7 ± 2.5	90.2 ± 2.5	91.0 ± 2.6	89.4 ± 2.5	88.5 ± 2.6	93.3 ± 2.5	95.1	-0.68 ± 1.04	
		F_{IS} = 0 response units									
Per se	96.5 ± 2.0	95.6 ± 2.0	93.0 ± 2.0	86.8 ± 2.0	85.4 ± 2.0	87.9 ± 2.0	87.8 ± 2.0	86.7 ± 1.9	104.4	-1.51 ± 1.04	*q*
		F_{IS} = 0.5 response units									
Per se	81.4 ± 3.9	79.5 ± 3.9	83.0 ± 3.9	75.8 ± 4.1	76.6 ± 3.9	75.9 ± 3.9	82.9 ± 3.9	82.2 ± 4.1	77.9	0.32 ± 2.06	
		F_{IS} = 0.75 response units									
Per se	81.4 ± 3.9	79.5 ± 3.9	83.0 ± 3.9	75.8 ± 4.1	76.6 ± 3.9	75.9 ± 3.9	82.9 ± 3.9	82.2 ± 4.1	88.3	-1.27 ± 1.25	*q*

q regression coefficients significant for quadratic effects at the 0.05 level of significance.

Supplemental Table A.3.6. Summary of mean pollen shed date ± standard errors (se) for multiple response units of BSSS and BS13(S), least square linear regression intercept at BS13(S)C0, BS13(S) linear regression coefficients, and significance of linear, quadratic, and cubic effects. Linear regression coefficients were computed as the average change per cycle. 95% C. I. = se * $t_{0.025,\ d.f.}$; $t_{0.025,\ 5} = 2.571$.

	BSSS	BS13(S) Cycle of selection							Regression coefficients for BS13(S)		
	C0	C0	C1	C2	C3	C4	C5	C6	b_0	b_1	*sig.*
	----------days after planting----------										
Testcrosses		Outbred response units									
Mo17	67.67 ± 0.45	67.67 ± 0.45	67.00 ± 0.45	66.33 ± 0.45	67.00 ± 0.45	67.00 ± 0.45	68.00 ± 0.45	67.67 ± 0.45	67.80	0.10 ± 0.18	*q*
B91	67.67 ± 0.45	65.67 ± 0.45	65.00 ± 0.45	66.00 ± 0.45	66.33 ± 0.45	66.67 ± 0.45	66.67 ± 0.45	66.00 ± 0.45	65.53	0.17 ± 0.23	
BS26	66.67 ± 0.45	67.67 ± 0.45	67.00 ± 0.45	65.00 ± 0.45	68.00 ± 0.45	67.67 ± 0.45	66.33 ± 0.45	67.67 ± 0.45	66.92	0.05 ± 0.30	
BSSS	69.67 ± 0.32	69.33 ± 0.45	68.67 ± 0.45	68.67 ± 0.45	68.67 ± 0.45	70.00 ± 0.45	68.67 ± 0.45	69.00 ± 0.45	68.98	0.01 ± 0.20	
BS13(S)C0	69.33 ± 0.45	69.83 ± 0.32	69.67 ± 0.45	69.00 ± 0.45	69.33 ± 0.45	69.67 ± 0.45	70.00 ± 0.45	70.00 ± 0.45	69.62	0.29 ± 0.14	
		F_{IS} = 0 response units									
Per se	69.67 ± 0.32	69.83 ± 0.32	70.00 ± 0.32	70.17 ± 0.32	70.00 ± 0.32	70.67 ± 0.32	70.83 ± 0.32	71.00 ± 0.32	69.62	0.24 ± 0.13	*l*
		F_{IS} = 0.5 response units									
Per se	71.60 ± 0.21	71.4 ± 0.21	71.4 ± 0.21	71.00 ± 0.21	71.4 ± 0.21	71.6 ± 0.21	71.00 ± 0.21	71.6 ± 0.21	71.30	0.01 ± 0.13	
		F_{IS} = 0.75 response units									
Per se	72.20 ± 0.29	72.00 ± 0.29	72.20 ± 0.29	72.00 ± 0.29	71.40 ± 0.29	73.60 ± 0.29	71.60 ± 0.29	72.20 ± 0.29	72.04	0.04 ± 0.18	

l, *q* regression coefficients significant for linear and quadratic effects respectively at the 0.05 level of significance.

Supplemental Table A.3.7. Summary of mean silk emergence date ± standard errors (se) for multiple response units of BSSS and BS13(S), least square linear regression intercept at BS13(S)C0, BS13(S) linear regression coefficients, and significance of linear, quadratic, and cubic effects. Linear regression coefficients were computed as the average change per cycle. 95% C. I. = se * $t_{0.025,\ d.f.}$; $t_{0.025,\ 5} = 2.571$.

	BSSS	BS13(S) Cycle of selection							Regression coefficients for BS13(S)		
	C0	C0	C1	C2	C3	C4	C5	C6	b_0	b_1	*sig.*
	----------days after planting----------										
Testcrosses		Outbred response units									
Mo17	71.33 ± 0.42	70.67 ± 0.42	70.33 ± 0.42	70.00 ± 0.42	70.00 ± 0.42	70.33 ± 0.42	70.33 ± 0.42	70.00 ± 0.42	70.37	-0.06 ± 0.13	
B91	69.33 ± 0.42	68.00 ± 0.42	68.00 ± 0.42	68.67 ± 0.42	68.67 ± 0.42	68.67 ± 0.42	68.67 ± 0.42	68.00 ± 0.42	68.19	0.05 ± 0.22	
BS26	70.67 ± 0.42	70.67 ± 0.42	70.67 ± 0.42	68.33 ± 0.42	70.00 ± 0.42	70.33 ± 0.42	68.67 ± 0.42	70.67 ± 0.42	70.07	-0.07 ± 0.25	
BSSS	73.33 ± 0.30	72.67 ± 0.42	72.33 ± 0.42	71.67 ± 0.42	72.33 ± 0.42	71.67 ± 0.42	71.67 ± 0.42	71.67 ± 0.42	72.41	-0.15 ± 0.16	
BS13(S)C0	72.67 ± 0.42	72.83 ± 0.30	72.33 ± 0.42	71.67 ± 0.42	72.67 ± 0.42	72.00 ± 0.42	72.67 ± 0.42	72.67 ± 0.42	73.21	-0.48 ± 0.12	*q*
Per se		F_{IS} = 0 response units									
BS13(S)	73.33 ± 0.30	72.83 ± 0.30	73.00 ± 0.30	72.33 ± 0.30	70.30 ± 0.30	73.00 ± 0.30	72.83 ± 0.30	73.00 ± 0.30	72.44	0.07 ± 0.11	
		F_{IS} = 0.5 response units									
BS13(S)	75.20 ± 0.19	74.04 ± 0.21	74.40 ± 0.19	74.00 ± 0.19	74.00 ± 0.19	74.00 ± 0.19	74.20 ± 0.19	74.20 ± 0.19	74.10	0.00 ± 0.09	
		F_{IS} = 0.75 response units									
BS13(S)	75.60 ± 0.26	75.40 ± 0.26	75.20 ± 0.26	74.20 ± 0.26	74.00 ± 0.26	75.80 ± 0.26	74.20 ± 0.26	74.20 ± 0.26	75.14	-0.14 ± 0.16	

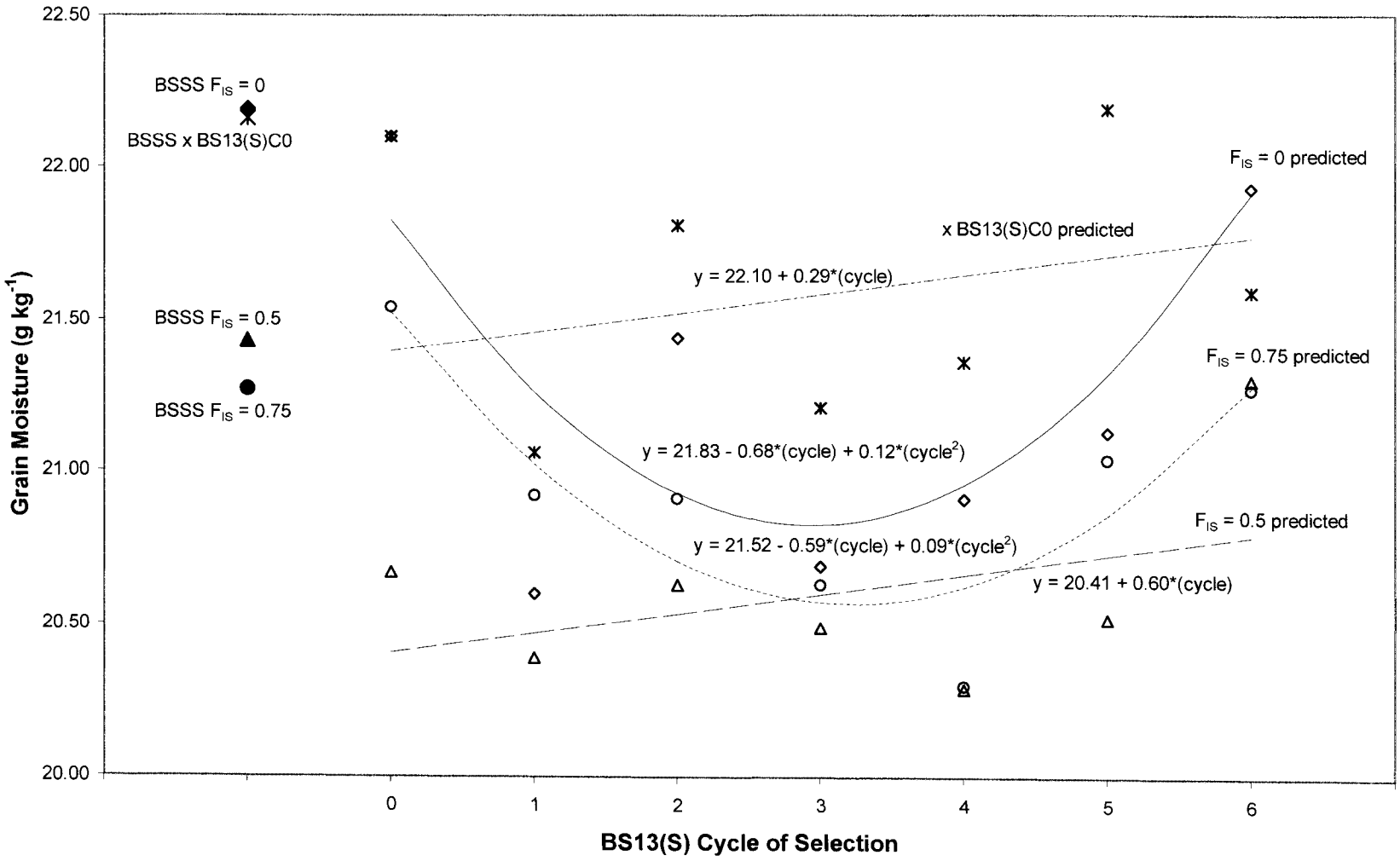
q regression coefficient significant for quadratic effects at the 0.05 level of significance.

Supplemental Table A.3.8. Summary of average proportional index ± standard errors (se) for multiple response units of BSSS and BS13(S), least square linear regression intercept at BS13(S)C0, BS13(S) linear regression coefficients, and significance of linear, quadratic, and cubic effects. Linear regression coefficients were computed as the average change per cycle. 95% C. I. = se * $t_{0.025,\ d.f.}$; $t_{0.025,\ 5} = 2.571$.

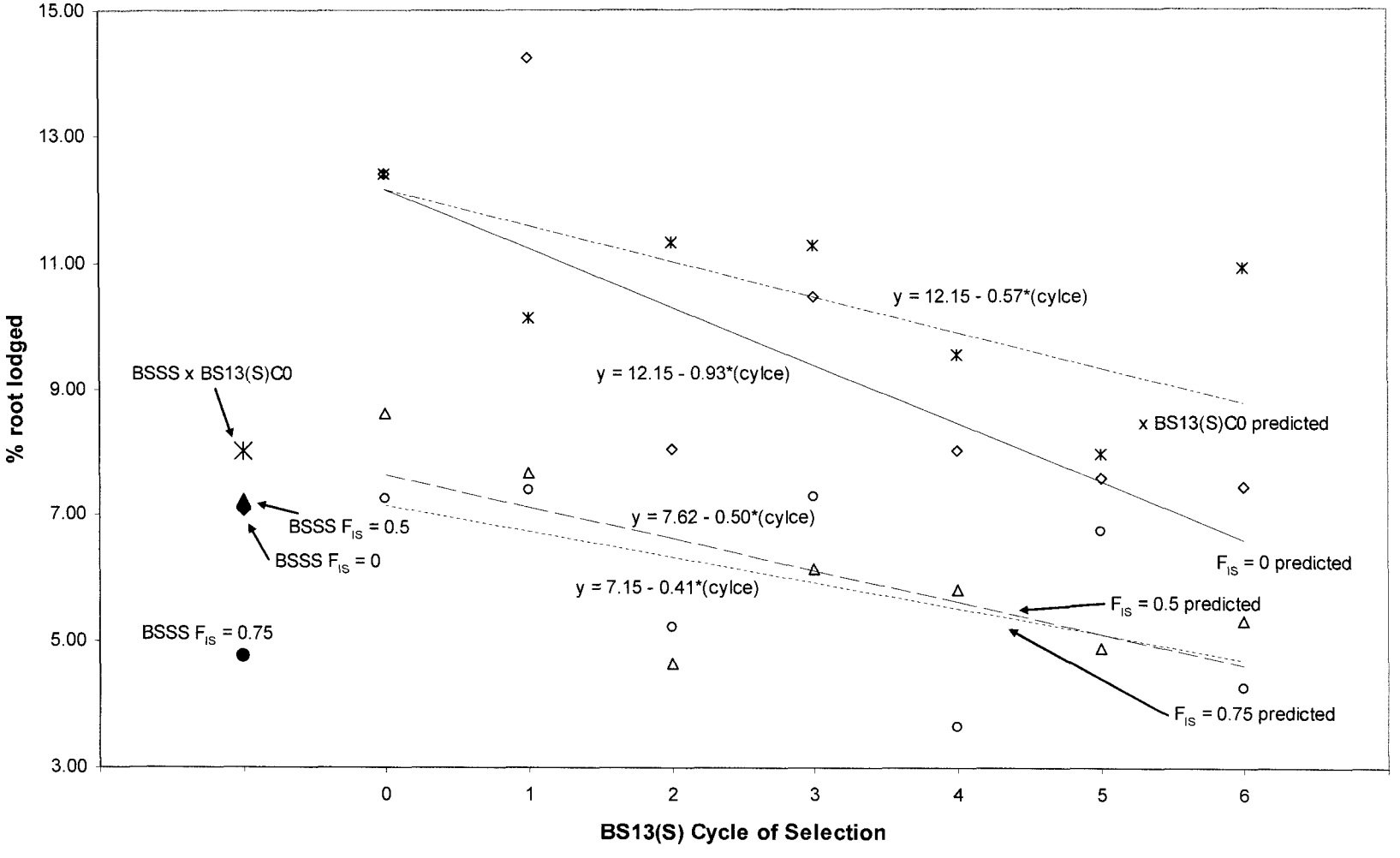
	BSSS	BS13(S) Cycle of selection							Regression coefficients for BS13(S)		
	C0	C0	C1	C2	C3	C4	C5	C6	b_0	b_1	*sig.*
	----------†Index----------										
Testcrosses		Outbred response units									
Mo17	39.61 ± 6.70	54.40 ± 6.38	48.42 ± 6.28	42.39 ± 6.28	51.27 ±6.28	52.51 ± 6.28	54.18 ± 6.55	52.61 ± 6.28	55.13	0.55 ± 1.27	*c*
B91	38.95 ± 6.38	43.43 ± 6.43	48.52 ± 6.28	45.17 ± 6.38	43.62 ± 6.43	44.65 ± 6.38	48.3 ± 6.28	51.26 ± 6.28	43.77	0.76 ±1.21	
BS26	22.41 ± 6.28	33.87 ± 6.28	38.88 ± 6.28	34.39 ± 6.28	36.89 ± 6.28	34.92 ± 6.38	41.43 ± 6.28	38.42 ± 6.43	34.47	0.67 ± 1.19	
BSSS	4.39 ± 5.20	24.31 ± 6.28	17.2 ± 6.28	21.7 ± 6.38	21.48 ± 6.28	21.97 ± 6.28	25.75 ± 6.28	25.17 ± 6.43	20.18	0.71 ± 1.26	
BS13(S)C0	24.31 ± 6.28	18.78 ± 5.20	22.78 ± 6.28	23.73 ± 6.28	25.00 ± 6.67	20.27 ± 6.28	22.38 ± 6.43	22.23 ± 6.28	18.66	0.77 ± 0.90	
		F_{IS} = 0 response units									
Per se	4.39 ± 5.20	18.78 ± 5.20	15.56 ± 5.26	18.12 ± 5.20	20.69 ± 5.26	16.08 ± 5.17	20.45 ± 5.24	19.9 ± 5.13	18.66	-0.01 ± 0.85	
		F_{IS} = 0.5 response units									
Per se	-4.53 ± 2.74	2.78 ± 2.81	11.54 ± 2.77	13.10 ± 2.82	13.68 ± 2.77	13.54 ± 2.74	15.67 ± 2.77	14.23 ± 2.77	4.56	1.53 ± 0.92	*q*
		F_{IS} = 0.75 response units									
Per se	-8.72 ± 2.88	3.78 ± 2.85	7.12 ± 2.95	7.80 ± 2.78	9.09 ± 2.92	13.03 ± 2.85	12.95 ± 2.88	10.03 ± 2.86	5.35	1.28 ± 0.92	*l*

l, q, c regression coefficient significant for linear, quadratic, and cubic effects at the 0.05 level of significance. †*Index = quintles - (h^2moisture/h^2quintles)*moisture - (h^2root lodging/h^2quintles)*root lodging - (h^2stalk lodging/h^2quintles)*stalk lodging.*

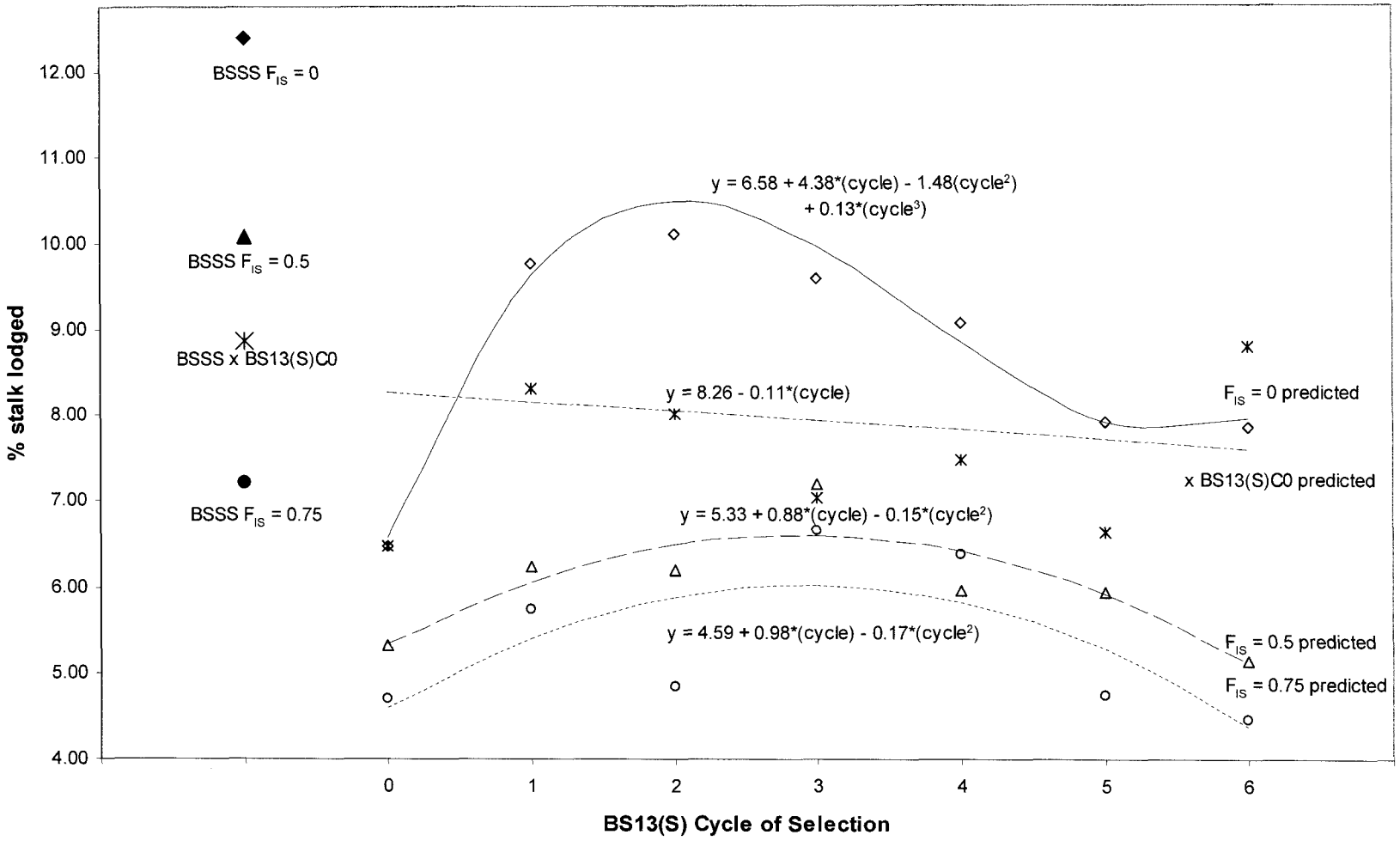
Appendix B. Supplemental Figures



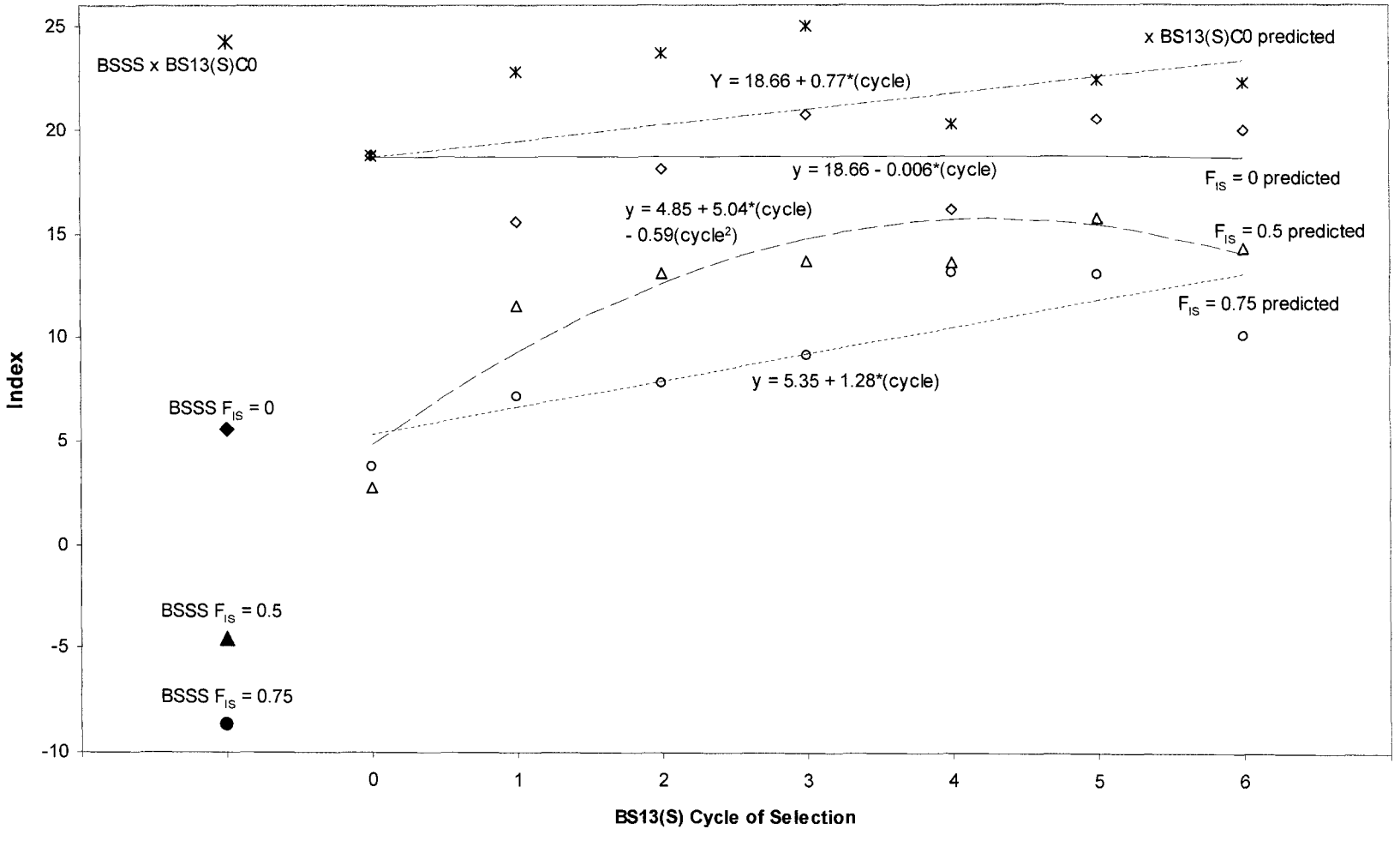
Supplemental Figure B.3.1. Observed values of BSSS and BS13(S) and predicted regressions of mean grain moisture on BS13(S)C0 and six cycles of S_2 progeny recurrent selection in the BS13(S) maize population for $F_{IS} = 0$, $F_{IS} = 0.5$, $F_{IS} = 0.75$, and BS13(S) x BS13(S)C0 populations. Quadratic regression coefficients were significant for the $F_{IS} = 0$ and $F_{IS} = 0.5$ populations.



Supplemental Figure B.3.2. Observed values of BSSS and BS13(S) and predicted regressions of mean root lodging on six cycles of S_2 progeny recurrent selection in the BS13(S) maize population for $F_{IS} = 0$, $F_{IS} = 0.5$, $F_{IS} = 0.75$, and BS13(S) x BS13(S)C0 populations. Linear regression coefficients were significant for the $F_{IS} = 0$ populations.



Supplemental Figure B.3.3. Observed values of BSSS and BS13(S) and predicted regressions of mean stalk lodging on six cycles of S_2 progeny recurrent selection in the BS13(S) maize population for $F_{IS} = 0$, $F_{IS} = 0.5$, $F_{IS} = 0.75$, and BS13(S) x BS13(S)C0 populations. Quadratic regression coefficients were significant for the $F_{IS} = 0.5$ and $F_{IS} = 0.75$ populations. Cubic regression coefficients were significant for the $F_{IS} = 0$ populations.



Supplemental Figure B.3.4. Observed values of BSSS and BS13(S) and predicted regressions of mean selection index on six cycles of S_2 progeny recurrent selection in the BS13(S) maize population for $F_{IS} = 0$, $F_{IS} = 0.5$, $F_{IS} = 0.75$, and BS13(S) x BS13(S)C0 populations. Linear regression coefficients were significant for the $F_{IS} = 0.75$ population. Quadratic regression coefficients were significant for the $F_{IS} = 0.5$ populations.

CHAPTER 4. S_2 PROGENY RECURRENT SELECTION IS INEFFECTIVE

A paper to be submitted for publication in Crop Science

Clinton J. Turnbull, Jode W. Edwards*, and Kendall R. Lamkey

Introduction

"One of the ways to increase gain from selection is to increase the additive genetic variance among families under evaluation" (Eberhart, 1970). Based on this presumption, increasing genetic gain from selection should be achieved by evaluating S_2 progeny as the additive genetic variance among progenies is increased by inbreeding progeny. The covariance among half-sib progeny equals $\frac{1}{4}\sigma_A^2$, the covariance among S_1 progeny equals $\sigma_A^2 + 1/4\sigma_D^2$ (Sprague and Eberhart, 1977), and the covariance among S_2 progeny equals $\frac{3}{2}\sigma_A^2 + \frac{3}{16}\sigma_D^2$ (Hallauer and Miranda, 1988).

Traditional recurrent selection methods were based on various forms of half-sib selection methods (Sprague, 1946; Jenkins, 1935; Hull, 1945). These recurrent selection programs select progeny with good general combining ability and self pollinated to a degree when they might be genetically stable. During the inbreeding process testcrosses were made with the selected progeny periodically, in an attempt to identify superior performing hybrids to be released as cultivars (Sprague, 1946). The gene actions controlling heterosis were outlined as complete dominance, overdominance, epistasis, or some combination thereof (Sprague and Eberhart, 1977). Multiple investigations of quantitative genetics were launched

to answer the question of gene action in maize (Gardner, 1963), Moll et al. (1964), Moll and Robinson (1967), Eberhart et al. (1966). These and other studies supported dominance as the most important form of gene action. Overdominance did not appear as important as dominance (Sprague and Eberhart, 1977 p. 326). Additionally, additive variance accounted for the major portion of the genetic variance (Eberhart et al., 1966) in maize populations. These findings of dominance being the leading cause of gene action and additive effects accounting for most of the variation among progeny were evidence that superior genotypes need not be hybrid cultivars and that support from the genetic gain equation (Comstock, 1964), a form of inbred progeny selection should be superior to other selection methods.

S_1 and S_2 progeny recurrent selection are two variations of inbred progeny recurrent selection methods which have been evaluated extensively in the literature (Turnbull et al., in review; Horner et al., 1989; Tanner and Smith, 1987; Horner, 1983; Horner et al., 1973). Among the studies outlined none have proven effective for long term response of the panmictic population.

Comstock (1964) adapted genetic gain prediction models developed from quantitative genetic theory (Lush, 1945). The superiority Eberhart (1970) and Comstock (1964) predicted has not been realized for inbred progeny recurrent selection programs for grain yield (Turnbull et al., in review; Lamkey, 1992; Horner et al. 1989; Iglesias and Hallauer, 1989; Tanner and Smith, 1987; Horner, 1983). Despite failure to support early genetic gain theory, the BS13(S) maize population has undergone ten cycles of S_2 inbred progeny recurrent selection spanning more than thirty years of selection.

The response unit targeted via the inbred progeny recurrent selection method is not clearly stated in the literature (Fehr, 1991; Hallauer and Miranda, 1988; Comstock, 1964).

The common assumption is that the panmictic population is the targeted response unit of inbred progeny recurrent selection. Due to the failure of realization of inbred progeny selection as an effective method of recurrent selection to improve panmictic population performance (Iglesias and Hallauer, 1989; Lamkey, 1992), the genetic gain equation has been recently decomposed (Wardyn et al., in review). The genetic gain equations presented by Wardyn et al. (in review) clearly address the selection unit and response unit. Directly defining the selection unit and response unit in relation to the genetic gain equation (Hanson, 1963) is critical ideology which has been discussed at length recently (Holland, 2003). The selection units are defined specific to the particular selection program (i.e. half-sib selection, full-sib selection, inbred progeny selection, etc.). The response unit may be any type of population genotype desired. When the response unit is defined specifically, the genetic gain equation may be used effectively to aid in determination of selection methods to employ and in which population genotype the greatest gains are expected.

Four types of genotypes are commonly evaluated as response units from recurrent selection programs to include: a panmictic population, an outbred population, a population with an expected average inbreeding level of $F_{IS} = 0.5$ in relation to their panmictic population (Wright, 1984), and a population with an expected average inbreeding level of $F_{IS} = 0.75$ in relation to their panmictic population (Wright, 1984). These response units are often referred to as S_0, testcross, S_1, and S_2 populations in the literature respectively. Interestingly, following the notation from Wardyn et al. (in review), genetic gain predictions applied to the BSCB1(R)C13 maize population genetic parameters for S_2 inbred progeny selection indicate that the rate of expected response is greatest for S_2 populations with less for S_1 populations and least for the S_0 populations. Prediction theory may not exactly be

realized (Wardyn et al., in review), predictions should however indicate proportional trends of the response units. Grain yield performance from S_1 and S_2 populations in the BS13(S)C0 maize population is less than the S_0 population due to inbreeding depression (Edwards and Lamkey, 2002). By using genetic variance components estimated for BS13(S)C0 (Edwards and Lamkey, 2002) in genetic gain prediction equations recently published (Wardyn et al., in review), grain yield performance from S_1 and S_2 progeny from latter cycles of BS13(S) are predicted to approach the performance of the S_0 population.

The objective of this study is to determine if the grain yield performance of the populations at $F_{IS} = 0.5$ and $F_{IS} = 0.75$ from BS13(S) after ten cycles of S_2 progeny recurrent selection are converging on the grain yield performance of the panmictic population as projected by realized response patterns after six cycles of S_2 progeny recurrent selection (Turnbull et al., in review) and recent advances in genetic gain theory (Wardyn et al., in review; Edwards and Lamkey, 2002). Additionally we would like to confirm the response patterns for other agronomic traits in the panmictic, outbred, and populations at $F_{IS} = 0.05$ and $F_{IS} = 0.75$ from BS13(S)C0-C10 with the response patterns found for BS13(S)C0-C6 (Turnbull et al., in review).

Materials and Methods

Genetic Materials and Selection Procedures

The Iowa stiff stalk synthetic maize population (BSSS(HT)) is a standard reference population for current maize breeders because of economically important parental inbred lines derived thereof. Its development in 1939 and population improvement methods have been outlined previously (Lamkey, 1992; Turnbull, in review). Due to an earlier era of

theory, the successful breeding method being utilized in BSSS(HT) (Smith, 1983) was changed in pursuit of a superior breeding method and at that time the population was renamed BS13(S) to indicate the former breeding method (using IA13 as the tester) and ('S' to indicate evaluation of selfed progeny) the type of progeny evaluated for the successive breeding method. IA13 is a double cross hybrid and when used as a tester it was to estimate general combing ability (Poehlman and Sleper, 1995). The progeny evaluated, progeny recombined, selection criteria, selection differentials, and heritabilities for BS13(S)C0 – BS13(S)C6 (where (*x*) designates the selection method and C*n* designates the n^{th} cycle of selection) have been summarized (Turnbull et al., in review). In the evaluation of BS13(S)C6 progeny a multiplicative selection index (Table 1) was used to make the selections, which included grain yield, grain moisture, root lodging, and stalk lodging. Progeny evaluation in BS13(S)C4-5 and BS13(S)C7 – BS13(S)C10 utilized a formal heritability selection index including selection for high grain yield, low grain moisture, low root lodging, and low stalk lodging. The heritability index is a summation index in which each trait is weighted by its corresponding heritability. Development of the BS13(S) population for cycle six through cycle ten has been summarized in Tables 1 and 2.

Experimental Procedures and Data Collection

Four types of genotypes were evaluated in this study 1) Panmictic populations, 2) outbred populations, 3) populations of unrelated individuals with an expected average inbred level in relation to the sub population of $F_{IS} = 0.5$ (Wright, 1984), 4) and populations of unrelated individuals with an expected average inbred level in relation to the sub population

of $F_{IS} = 0.75$ (Wright, 1984). $F_{IS} = 0.5$ and $F_{IS} = 0.75$ in the literature is often referred to as S_1 and S_2 populations respectively.

The panmictic populations were developed from intermating all combinations of superior individuals from the BS13(S)C_{n-1} population via the bulk entry diallel method (Fehr, 1991 p. 147) followed in another season by random mating 85-250 bulk diallel progeny. The outbred populations were developed from a random sample of the panmictic population cross pollinated with one of three testers. The three testers used to develop the outbred populations were IA13, B97 (Hallauer et al., 1994), and TR7322 (an elite industry Mo17-Oh43 type parental line). The population of individuals with an expected $F_{IS} = 0.5$ were developed from self pollinating a random sample of 56 -170 individuals from the panmictic population for one generation. The population of individuals with an expected $F_{IS} = 0.75$ were developed from self pollinating a random sample of 46 -193 individuals from the panmictic population for two generations.

This study was composed of three separate experiments all containing materials from BSSS, BSSS(HT)C7, and each BS13(S)C0 - BS13(S)C10. The first experiment consisted of treatments of panmictic population genotypes and outbred population genotypes and will be referred to as the non-inbred experiment. The second experiment consisted of treatments of genotypes with expected $F_{IS} = 0.5$ and will be referred to as the $F_{0.5}$ experiment. The third experiment consisted of treatments of genotypes with expected $F_{IS} = 0.75$ and will be referred to as the $F_{0.75}$ experiment. Because plant vigor is reduced with inbreeding (Shull, 1908) it was important to separate treatments into these three separate experiments to minimize plant competition between treatments of varying levels of inbreeding. Treatments

were replicated three times within each environment. Treatments containing BS13(S)C0 and BS13(S)C9 material were represented twice in each replicate of the experiments.

All experiments were evaluated in 2002 at eight environments including six Iowa environments (Ames, Ankeny, Carroll, Crawfordsville, Fairfield, and Rippey), one Nebraska environment (Minden), and one Illinois environment (Mt. Pulaski). The experiments were also evaluated in 2003 at ten environments including eight Iowa environments (Ames, Ankeny, Carroll, Crawfordsville, Fairfield, Lewis, and Rippey), two Nebraska environments (Fremont and Tekamah), and one Illinois environment (Havana). In 2005 the non-inbred and $F_{0.5}$ experiments were grown at three Iowa environments (Ames, Ankeny, and Fairfield). Three replications per location were grown for each of the experiments.

Due to poor stands at Ankeny in 2003 for the $F_{0.5}$ and $F_{0.75}$ experiments, this location data was excluded from the analysis of these two experiments. Due to seed shortages the $F_{0.75}$ experiment was not grown in 2005.

Experimental units for agronomic evaluations were field plots two rows 5.47 m long with 0.76 m between rows. Plots in 2002 and 2003 were overplanted and thinned to uniform stands of ≈ 67,000 plants ha^{-1} and ≈ 62,200 plants ha^{-1} in 2005. The lower final plant density in 2005 was an attempt to reduce stalk lodging at harvest. All plots were machine planted and machine harvested. Data for grain yield (t ha^{-1}), grain moisture (g kg^{-1}), root lodging (percentage of plants inclined more than 30 ° from vertical), stalk lodging (percentage of plants broken at or below the ear node), ear height (cm), plant height (cm), and 50% silk emergence were collected. The number of environments and data collected is summarized in Table 3. Ear and plant heights were calculated as the average of measurements for ten competitive plants per plot and measured as the distance from the soil surface to the highest

ear-bearing node (ear height) and the node of the flag leaf (plant height). When data were collected at an environment, three replications were collected with the exceptions for plant and ear heights at Minden, Nebraska, in the non-inbred experiment in 2002 and root and stalk lodging at Fairfield in 2005. In these two instances only two replications of data were collected.

Statistical Methods

Transforming Data

Because of the use of a heritability selection index as selection criteria in the later cycles of BS13(S) (Table 1) and because heritability varies with the level of inbreeding (Holland, 2003) , a measure of it's response in the population at $F_{IS} = 0.75$ may be considered a direct response to selection. In an attempt to measure the direct response to selection a realized index was developed similarly to methods used in Turnbull et al. (in review). Due to the lack of use of the heritability index in every cycle of advancement true selection index coeffecients are unattainable and our average-index is a valid substitute.

Analysis of the Data

Individual environment analyses were conducted based on a linear additive model including replications and treatments as main effects for the $F_{0.5}$ and $F_{0.75}$ experiments. The non-inbred experiment was analyzed similarly with the addition of row and column within replications as additional main effects in the model. The data were analyzed with main effects considered fixed effects blocking on replications or row and column within replication as appropriate. These individual environment analyses were conducted in order

to test for outlier data via the Anscombe-Tukey test for outliers (Anscombe and Tukey, 1963). Caution was used in removing data from the dataset by only removing clearly detected outliers with plausible explanations that met the threshold value.

Once the individual environmental data was checked for outliers a similar linear additive model was developed to calculate overall treatment means and corresponding standard errors within each of the three experiments (non-inbred experiment, $F_{0.5}$ experiment, and $F_{0.75}$ experiment). The model follows:

$y = env + rep(env) + row(rep * env) + column(rep * env) + treatment + env * treatment$. Row and column effects are excluded in the $F_{0.5}$ and $F_{0.75}$ experiments as they are only blocked on replications. The main effects were considered as fixed effects. The treatment X environment interaction was considered a random effect and used as the treatment variance to calculate appropriate standard errors. A pooled error was considered random and used as to make a conservative test of the treatment X environment effect. Treatment means were adjusted for the environment, replication, row, and column effects according to standard least squares mean procedures (Steel et al., 1997). The standard errors of the means were calculated for the entries as the square root of the entry variance divided by the number of observations in the mean ($s_{\bar{Y}} = \sqrt{\frac{\sigma^2}{n}}$). The parity in number of observations is due to the number of replications for particular treatments in the experiment caused by the unbalanced treatment design, outlier data treated as missing data, or missing data for some of the replications as previously outlined.

A particular interest in this study was to model the pattern of response across cycles of selection in of BS13(S)C0-C10 for each of the types of genotypes over all environments.

Additionally comparison tests of BSSS vs. BSSS(HT)C7, BSSS vs. BS13(S) intercept at cycle 0, and BSSS(HT)C7 vs. BS13(S) intercept at cycle 0 were of interest.

To model the pattern of response for each of the types of population genotypes, a covariate mixed model was developed. This is a very similar model to the one used to calculate treatment means with the addition of the cycle within each genotype. The treatments and treatment X environment interaction however, were considered random effects in the model. The treatments were included as random effects to account for the random deviations of the population from the regression due to random genetic effects found in the various cycles of the populations. Cycle within genotype was the covariate. Testing for quadratic and cubic responses were conducted by including appropriate higher order levels of cycle in the model. Predicted values for the model which fit the data significantly for each genotype were plotted against cycles (Figures. 4.1 and 4.2 and supplemental figures B.4.1 – B.4.8).

A similar covariate model was developed replacing the cycle of selection with the cumulative selection differential. The selection differential is the mean of the progeny evaluated subtracted from the mean of the progeny selected at each cycle of selection. The cumulative selection differential is the sum of the prior selection differentials ($Cn + Cn\text{-}1 + \ldots + Cn\text{-}n$). Regressing the means on cumulative selection differentials gives a direct interpretation of response observed to the amount of effort used in the formation of the cycles of the population. The linear response of this regression is the realized heritability (h^2) throughout the history of the BS13(S) program (Hanson, 1963).

Results

The averages for grain yield across environments were highest in the non-inbred experiment, followed by the $F_{0.5}$ and $F_{0.75}$ experiments respectively as expected. The cycle means for grain yield are reported in table 4. Grain yield of the Panmictic population did not respond to inbred progeny selection (Table 4). The grain yield intercept for BS13(S)C0 from the covariate model was 4.94 t ha^{-1} and at BS13(S)C10 was 5.08 t ha^{-1} (Table 3). Interestingly, the deviations from the regression are much greater in the early cycles of selection than the latter ones. There are significant differences between BSSS and BSSS(HT)C7 panmicitic populations for grain yield with an average response of 0.18 t ha^{-1} per cycle (Table 4).

Grain yield of the population at $F_{IS} = 0.5$ responded favorably in the BS13(S) population with quadratic effects explaining the response pattern (Table 4 and Fig. 1). The average response for grain yield of the BS13(S) population at $F_{IS} = 0.5$ was 0.09 t ha^{-1} per cycle with an intercept at BS13(S)C0 of 4.14 t ha^{-1}. Differences between BSSS and BSSS(HT)C7 for the populations at $F_{IS} = 0.5$ are significant with an average response of 0.16 t ha^{-1} per cycle (Table 4).

Grain yield of the population at $F_{IS} = 0.75$ responded most favorably of all the population genotypes in the BS13(S) population with linear effects explaining the response pattern (Table 4 and Fig. 1). The average response per cycle for this population was 0.12 t ha^{-1} per cycle with an intercept at BS13(S)C0 of 3.74 t ha^{-1}. Differences between BSSS and BSSS(HT)C7 for the populations at $F_{IS} = 0.75$ are significant with an average response of 0.18 t ha^{-1} per cycle (Table 4).

Grain yield for all three outbred populations did not respond favorably to inbred progeny selection (Table 4). Linear effects did explain the response pattern of the BS13(S) populations when outbred with IA13 and B97 however, the average responses in both populations were minimal at 0.04 t ha^{-1} per cycle (Table 4 and Fig. 2). No response was detected when BS13(S) was outbred with TR7322. The grain yield intercept at BS13(S)C0 was 5.42 t ha^{-1}, 7.58 t ha^{-1}, and 8.87 t ha^{-1} for the IA13, B97, and TR7322 outbred populations respectively. Differences between BSSS and BSSS(HT)C7 for all three outbred populations were significant. The average responses from BSSS to BSSS(HT)C7 were 0.11 t ha^{-1}, 0.11 t ha^{-1}, and 0.14 t ha^{-1} per cycle for the IA13, B97, and TR7322 outbred populations respectively.

BSSS(HT)C7 and the intercept for BS13(S)C0 were not significantly different for any of the population genotypes for grain yield (Table 4).

The standardized-relational index responded favorably with linear effects explaining the response pattern for all population genotypes with exception to the TR7322 outbred population. As the level of inbreeding increases, the average response per cycle of the index increases. The test comparing the indexed values of BSSS and BSSS(HT)C7 were significant for all population genotypes. In comparing indexed values of BSSS and the intercept at BS13(S)C0, the IA13 outbred population is the only non-significant test (Supplemental table 1). The plant stand responded favorably in the panmictic population, $F_{0.5}$ population of individuals, and $F_{0.75}$ population of individuals with linear effects explaining the response patterns. Plant stand revealed a similar trend as the index with the average response per cycle increasing with increasing level of inbreeding. The test between BSSS and the BS13(S) intercept at cycle zero in the B97 outbred population was the only

significant test for plant stand. Grain moisture responded favorably in all population genotypes with exception of the B97 outbred population where no response was detected (Table 5). Though the grain moisture responses were favorable for nearly all the response units (Fig. 3), various response patterns explained significant portions of the observed variation within particular response units (Table 5). The mean grain moisture for the outbred populations were lower than that for the panmictic population, the population at F_{IS}= 0.5, and the population at F_{IS} = 0.75 (Supplemental table 2 and supplemental fig. 4). In all cases the latter cycles of BS13(S) appear to have greater affects in the favorable direction on the response pattern than the earlier cycles (Fig 4). Grain moisture was not changed in the BSSS(HT) program as seen by none of the response units of BSSS versus BSSS(HT)C7 comparisons being significant. Neither was there a significant change for grain moisture between BSSS(HT)C7 and BS13(S)C0 for any of the response units (Supplemental table 4). Root and stalk lodging responded favorably in all population genotypes (Table 5, supplemental fig. rtldg, and supplemental fig. skldg). Linear effects accounted for the response patterns for root lodging in the B97 outbred population, IA13 outbred population, panmictic population, and $F_{0.5}$ population of individuals (Table 5). Quadratic effects explained the response pattern of variation for root lodging in the $F_{0.75}$ population of individuals (Table 5). When comparing the population at F_{IS} = 0.5 to BSSS, BSSS(HT)C7 and BS13(S) are both significantly different for root lodging (Supplemental table 3). Linear, cubic, and quadratic effects explain the response patterns for stalk lodging of the panmictic population, the population at F_{IS} = 0.5 population, and the population at F_{IS} = 0.75 respectively (Table 5). Stalk lodging did not change from BSSS to BSSS(HT)C7 however, significantly higher stalk lodging did occur at the BS13(S)C0 intercept than either BSSS or

BSSS(HT)C7 for the panmictic population (Supplemental table 4). Similarly, stalk lodging in the population at F_{IS} = 0.75 was significantly higher at the BS13(S)C0 intercept than BSSS(HT)C7 (Supplemental table 4). Though statistical tests were not conducted to compare predicted values of the various population genotypes for root lodging, the intercept at BS13(S)C0 and average of BS13(S) predicted values of the regression for root lodging was notably less for the TR7322 outbred population when compared with the other two outbred populations (Supplemental table A.4.2). Similarly stalk lodging was notably more severe for the IA13 outbred populations at the intercept of BS13(S)C0 and average of BS13(S) predicted values from the regression than the TR7322 and B97 outbred populations (Supplemental tables A.4.3).

Ear heights for all population genotypes showed a negative response with linear effects accounting for the variation within the population genotypes (Table 5). Plant and ear height regression coefficients when only the linear term for cycle was included in the covariate model were nearly identical (Table 5). Responses of plant heights were linear with exception to the two inbred populations whose patterns of response were explained by quadratic effects for the population at F_{IS}= 0.5 and cubic for the population at F_{IS}= 0.75 (Table 5). Flowering dates for all population genotypes responded by flowering earlier at the latter cycles of BS13(S). The IA13 outbred population, panmictic population, the populations at F_{IS} = 0.5, and populations at F_{IS}= 0.75 patterns of variation for flowering date were all explained by linear effects (Table 5). Additionally the flowering dates in the panmictic population and population at F_{IS} = 0.5 did significantly become earlier from BSSS to BSSS(HT)C7. The comparative test of significance revealed a difference between

BSSS(HT)C7 and BS13(S) at the cycle zero intercept for silking date in the TR7322 outbred population (Supplemental table 5) but not between BSSS and BSSS(HT)C7.

The effort of selection as measured in the cumulative selection differential is strong and most consistent for grain yield across the ten cycles of BS13(S). Selection for root lodging mimics the selection effort for grain yield with a little less consistency. When used, the selection index is strong and very consistent. Selection effort placed on grain moisture and stalk lodging have been inconsistent however, very strong in the last few cycles of selection. The cumulative selection differentials as a percent of the BS13(S)C10 cumulative selection differential is plotted against cycle of selection in Figure 3.

Calculation of realized heritabilities (h^2) from the cumulative selection differential covariate analysis by regressing the trait of interest on the cumulative selection differentials for that trait reveals some key findings. The two inbred populations show the largest h^2 for grain yield. All of the non-inbred populations show either minimal h^2 or zero when considering grain yield. The h^2 for grain yield of the panmictic and inbred populations are significant and nearly equal however, minimal for the outbred populations. The h^2 for root lodging is strongest in the panmictic, IA13 outbred, and B97 outbred populations. Realized heritability is likely less in the other population genotypes as an artifact of lower initial (BS13(S)C0) root lodging values in those populations making it more difficult to maintain large reductions of root lodging per unit of cumulative selection differential. The change in h^2 for stalk lodging was strongest in the panmictic population. Interestingly it was not as strong in the IA13 outbred population as might be expected based on similar ideas as previously mentioned for root lodging as the IA13 outbred population is the most severly

stalk lodged population genotype. Realized heritabilities for the traits under selection are reported in table 6.

Discussion

Sprague and Eberhart (1977) did indicate that unless dominance effects are negligible, the improvement in the population per se cannot be predicted exactly. If the dominance effects are not negligible then the predicted improvement should be expected in a random set of S_1 lines.

The BS13(S) population is an improved population having BSSS as its progenitor population. The processes and procedures involved in forming BS13 from BSSS have recently been outlined in Turnbull et al. (in review). The response of grain yield for the panmictic population of BSSS(HT) have been favorable in previous studies with average rates of response per cycle being 0.164 t ha^{-1}, 0.074 t ha^{-1}, 0.344 t ha^{-1}, across seven cycles of selection (Lamkey, 1992; Helms et al., 1989; and Eberhart et al., 1973) and 0.183 t ha^{-1} in this study (Table 4). It was shown previously that grain yield gains in the panmictic population of BS13(S) did not respond favorably with an average rate of response per cycle across six cycles of selection being 0.024 t ha^{-1} and 0.009 t ha^{-1} (Turnbull et al., in review and Lamkey, 1992) and 0.014 t ha^{-1} across ten cycles of selection in this study (Table 4). This study and Lamkey (1992) support Turnbull et al. (in review) in that inbred progeny selection for the improvement of grain yield in the population per se is ineffective.

Our primary objective was to determine if the grain yields of inbred populations of BS13(S) are approaching the grain yields in the panmictic population after ten cycles of S_2 progeny recurrent selection. Though the various population genotypes were not analyzed in

a common experiment, they were analyzed in common environments and one can compare the predicted values at BS13(S)C9 and BS13(S)C10 (Fig. 1). Without conducting statistical tests of significance, all three generations from the population have essentially converged (Fig. 1). Additionally it appears that the $F_{0.5}$ inbred generation has reached an asymptote and may not be expected to exceed the performance of the panmictic population. The response pattern of the population at F_{IS}= 0.75 does not show any curvature and does not appear to have reached a maximum performance level. The average grain yield response per cycle of selection for BS13(S)C0-C10 are comparable to those reported for BS13(S)C0-C6 (Turnbull et al., in review) for the panmicit population and inbred populations. The patterns of responses are nearly identical between the two studies. However, the quadratic model explaining the variation of the population at F_{IS} = 0.5 for the previous study appears to have a maximum meniscus at BS13(S)C4 (Turnbull et al., in review) and this study appears to have a maximum meniscus at BS13(S)C8. This difference is likely due to the end points having a stronger effect on the regression than intermediate points, which in both cases the end points do not have the highest observed values, and thus pulling the regression curve slightly negative. Possibly an asymptotic model is more appropriate when modeling the response pattern if quadratic effects are significant. Grain yield in the outbred populations from this study and Turnbull et al. (in review) similarly show no or minimal response to S_2 progeny recurrent selection regardless of the tester. Plant stand response has not been directly selected for however, the response appears to mimic grain yield response (Table 4.4) as a correlated response to grain yield. The panmictic populations show no response while the population at F_{IS} = 0.75 shows the greatest average response per cycle (Table 4.4). Cold germination was selected for between the BSSS(HT)C7 and BS13(S)C0 (Turnbull et al. in

review). Cold germ tests were likewise improved however, BSSS(HT)C7 and the BS13(S)C0 intercept are not different indicating that one cycle of selection was ineffective for improvement of either plant stand and cold germination resistance. Continued selection of progeny for grain yield may be effective in improving cold germination tolerance.

Turnbull et al. (in review) concluded that lack of favorable responses of grain moisture to slection was due to inconsistent selection pressure and difficulty selecting for this trait. Since BS13(S)C6, a much more consistent selection pressure has been placed on grain moisture (Fig. 3), and the favorable responses clearly indicate this (Table 4 and supplemental fig. ?).

Root lodging average responses per cycle are nearly identical for all population genotypes in the BS13(S)C0-C6 (Turnbull et al., in review) and BS13(S)C0-C10 (Table 4). The observation in the population at $F_{IS} = 0.75$ BS13(S)C6 in this study (Supplemental figure B.4.2) appears to be an outlier and causes quadratic effects to be significant. When this point is removed, the pattern of response becomes strongly linear with an average response per cycle of -0.59 % root lodging.

Stalk lodging responds to selection pressure in the panmictic and inbred populations. This was also observed in the previous study (Turnbull et al., in review). The non-linear patterns of response in the inbred populations are likely explained by the very short plant stature and already low percentages of lodging. Likely selection pressure will need to increase to have a continued effect in decreasing both root and stalk lodging. Less pressure is required to maintain current lodging values.

Plant and ear heights have dramatically been reduced from BS13(S)C6-C10 in the panmictic population (Supplemental figures B.4.6 and B.4.7). Additionally, the observed

plant heights, ear heights, and phnotypic plant stature in the panmictic population variation within BS13(S)C9 and BS13(S)C10 and between them is visually much less than any of the other cycles of selection. Because plant and ear heights are unselected, this may be an indication of loss of genetic variance in the population. It is unclear whether plant and ear heights are a correlated trait to selection or due rather, to inbred depression. It may be argued to be from inbreeding depression as we see decreasing plant stature between the panmictic population, the population at $F_{IS} = 0.5$, and the population at $F_{IS} = 0.75$ as we know that the expected F_{ST} is increasing (Table 4.2).

Silking dates between this and Turnbull et al. (in review) do not show consistent trends. This is likely due to lack of evaluation in multiple environments in the previous study and for the $F_{IS} = 0.75$ response unit in this study (Table 4.3). Results from this study (Table 4) show that the non-outbred populations flower earlier across cycles of selection. This may be due to the two-stage selection process in this selection program. In developing S_2 families ($F_{IS} = 0.75$) for replicated evaluation, the later flowering S_1 families ($F_{IS} = 0.5$) are selected against in an attempt to counter-act the positive correlation often seen for grain yield and physiological maturity. If this correlation is not addressed, varieties developed may be unadapted for Iowa climates in extreme growing season (i.e. early frost, etc.).

The index in this study shows a clear trend with strongest responses in the population at $F_{IS} = 0.75$ and weaker responses in the panmictic population yet still significant (Table 4). following a similar trend to grain yield indicating that yield has consistently been most strongly selected.

Conclusion

Recurrent selection must be effective in one of two ways to be justified. They are 1) to improve the performance of the panmicitc population or 2) to improve the performance of hybrids developed from the population per se via a population cross or a single cross hybrid. Based on our data, neither has been successful. S_2 progeny recurrent selection is ineffective for improvement of grain yield in outbred and panmitic populations.

Though it is true that high performing inbred progeny may be expected to be developed from the latter cycles of selection of BS13(S), they will likely not exceed performance of the panmictic population (Edwards and Lamkey, 2002) due to pseudo-overdominace. Pseudo-overdominance is a condition which on the surface causes a population to respond similarly to overdominance (Hull, 1952) due to increasing linkage disequilibrium. Comstock's (1964) primary explaination for failure of inbred progeny selection was if overdominant gene action was important in the population. The dominance theory early inbred selection theory was based on (Comstock, 1964) is still the leading theory for corn breeding (Lamkey and Edwards, 1999). Pseudo-overdominance supports dominance theory (Edwards and Lamkey, 2002). Pseudo-overdominance may be overcome through creating linkage equilibrium via repeated random mating or other methods to disrupt linkage blocks. An experiment to create linkage equilibrium in early and latter cycles of this population to test this hypothesis of pseudo-overdominance would be most fitting.

A loss of genetic variance was forecast for BS13 (Eberhart, 1973) and thus the change from recombining ten to twenty was implemented to mitigate this loss. An expected F_{ST} (Wright, 1984) at BS13(S)C10 is approximately 0.62 (Table 4.2). Edwards and Lamkey (2003) do not predict gains to be effected in recurrent selection programs until F_{ST}

approaches 0.6. Holthaus and Lamkey (1995) estimated no loss of additive variance in the BS13(S) C6 from BS13(S)C0 and minimal loss of total genetic variance. Because of the hearsay concern of severe inbreeding in the panmictic population of latter cycles of BS13(S), it would be of interest to estimate additive and dominance variances at multiple cycles in the population. This population is a prime candidate to estimate σ^2_A, σ^2_D, and D1 (Harris, 1964) at multiple cycles from which to test selection gains models derived from Harris' genetic parameter model (1964). Additionally, correlations of inbred-outbred progeny would be readily available to further support lack of response if found to be low as suggested by Turnbull et al. (in review). Reporting the variance components for latter cycles would additionally refute or support the hearsay concern of severe inbreeding in the BS13(S) panmictic population.

We do not suggest using an inbred progeny selection method alone as a means for germplasm improvement. It may be appropriate to use this selection method in tandem with some form of testcross selection. Inbred progeny selection may be most effective if used in a system when adapting exotic materials. It may have a greater impact on reducing lodging more quickly than testcross evaluation methods alone in such a system. Additionally, improving inbred per se performance often required in exotic populations to develop inbred lines worthy as potential hybrid parent candidates may be achieved while simultaneously improving combining ability, reducing additional cycles of recombination with elite germplasm.

Table 4.1. Summary of the selection differentials, type of selection index, repeatabilities, and year of progeny evaluation trials used in evaluating progeny of indicated cycles in the BS13(S).

		‡Selection Differential						¶Repeatability				
Cycle of Selection	†Location of Progeny evaluations	Yield	Moisture	Root Lodging	Stalk Lodging	Index	§Type of selection Index	Yield	Moisture	Root Lodging	Stalk Lodging	Year of progeny evaluation
		t ha^{-1}	g Kg^{-1}	%	%			t ha^{-1}	g Kg^{-1}	%	%	
0	Ames, Ankeny, Martinsburg	1.39	-8.0	-6.2	1.0	NA	None	0.81	0.87	0.49	0.18	1972
1	#Ames, Ames, Martinsburg	1.75	2.0	-7.7	0.5	NA	None	0.67	0.87	0.69	0.43	1975
2	Ames, Ankeny, Martinsburg	1.03	2.0	0.5	2.5	NA	None	0.69	0.82	0.54	0.57	1978
3	Ames, Martinsburg, Columbia	1.12	-9.0	-0.1	-1.0	5.5	Unknown	0.51	0.66	0.24	0.33	1981
4	Ames, Ankeny, Martinsburg	0.64	-2.0	-4.3	-5.4	9.4	Heritability	0.73	0.74	0.15	0.72	1984
5	Ames, Ankeny, Martinsburg	1.40	5.0	-1.9	-2.2	11.9	Heritability	0.59	0.75	0.64	0.72	1987
6	Ames, Ankeny, Martinsburg	0.65	-4.0	-0.8	-5.5	149.6	Multiplicative	0.71	0.87	0.20	0.65	1990
7	Ames, Ankeny, Crawfordville	0.86	-8.0	-3.1	-3.0	9.4	Heritability	0.75	0.82	0.18	0.61	1993
8	Ames, Crawfordville, Carroll	0.82	-5.0	-3.7	-2.9	10.0	Heritability	0.74	0.85	0.32	0.80	1997
9	Ames, Crawfordsville, Carroll, Rippey	0.46	0.1	0.0	-11.0	15.5	Heritability	0.85	0.85	0.00	0.74	2000
10	Ames, Crawfordsville, Fairfield, Carrol, Rippey	0.63	-0.1	0.0	-0.1	6.5	Heritability	0.72	0.85	0.04	0.03	2003

†Ames, Ankeny, and Martinsburg are Iowa locations and Columbia is a Missouri location. Two replications evaluated at each location.

‡The difference of the mean of the selected individuals and the mean of all individuals.

§A weighted summation index where the traits are weighted by their corresponding heritability. A multiplicative index is where the mathematical product of the selected traits is the index. In this case truncation values were assigned and the multiplicative index = (Yield-30.6)*(Moisture-22.8)*(14.9-Root lodging)*(23.8-Stalk lodging).

¶Ratio of genetic variance to total variance.

#Two field locations near Ames; one at the agronomy farm and one at the atomic energy farm.

Table 4.2. Summary of the selection units, recombination units, number of progeny recombined and evaluated, selection intensity, and expected level of inbreeding used in evaluating progeny of indicated cycles in the BS13(S) maize population.

Cycle of selection	Selection unit	Recombination unit	Number of progeny		Selection Intensity	Expected F_{ST}
			Recombined	Evaluated		
0	S_2	S_2	10	100	0.10	0.39
1	S_2	S_2	10	100	0.10	0.45
2	S_1	S_1	20	100	0.20	0.47
3	S_2	S_1	20	100	0.20	0.49
4	S_2	S_1	20	100	0.20	0.51
5	S_2	S_1	20	150	0.13	0.53
6	S_2	S_2	20	129	0.16	0.55
7	S_2	S_2	20	169	0.12	0.58
8	S_2	S_2	20	150	0.13	0.61
9	S_2	S_2	20	120	0.17	0.63
10	S_2	S_2	20	130	0.15	0.66

Table 4.3. Total number of environments data were collected from for the traits indicated.

Experiment	Type of data collected						
	Grain Yield	Grain Moisture	Root Lodging	Stalk Lodging	Plant Height	Ear Height	Silking Date
	----------Number of environments----------						
Non-Inbred	21	21	20	20	12	12	2
$F_{0.5}$	20	20	19	19	12	12	2
$F_{0.75}$	18	18	17	17	9	9	1

Table 4.4. Summary of mean grain yields ± standard errors (se) for multiple response units of BSSS(HT) and BS13(S), linear regression coefficients, significance of linear, quadratic, and cubic effects, and tests of differences between indicated populations.

Population	Response units			Testcross response units		
	$F_{IS} = 0$	$F_{IS} = 0.5$	†$F_{IS} = 0.75$	IA13	B97	TR7322
	t ha^{-1}					
BSSS	3.60 ± 0.15	2.88 ± 0.13	2.57 ± 0.14	4.65 ± 0.17	6.74 ± 0.18	7.80 ± 0.16
BSSS(HT)C7	4.86 ± 0.16	4.02 ± 0.13	3.80 ± 0.13	5.61 ± 0.18	7.71 ± 0.18	8.82 ± 0.18
BS13(S)C0	4.70 ± 0.15	3.84 ± 0.11	3.66 ± 0.11	5.42 ± 0.17	7.77 ± 0.15	8.89 ± 0.16
BS13(S)C1	5.19 ± 0.18	4.08 ± 0.13	3.61 ± 0.13	5.50 ± 0.17	7.62 ± 0.16	8.84 ± 0.17
BS13(S)C2	5.33 ± 0.18	4.62 ± 0.13	4.20 ± 0.13	5.58 ± 0.18	7.59 ± 0.18	8.68 ± 0.18
BS13(S)C3	4.81 ± 0.18	4.67 ± 0.13	4.22 ± 0.13	5.43 ± 0.18	7.51 ± 0.17	9.09 ± 0.18
BS13(S)C4	4.73 ± 0.18	4.55 ± 0.13	4.30 ± 0.13	5.74 ± 0.18	7.79 ± 0.18	8.71 ± 0.18
BS13(S)C5	5.13 ± 0.18	4.74 ± 0.13	4.46 ± 0.13	5.68 ± 0.18	8.03 ± 0.18	9.04 ± 0.18
BS13(S)C6	5.03 ± 0.18	4.53 ± 0.13	4.48 ± 0.13	5.35 ± 0.18	7.89 ± 0.18	9.02 ± 0.18
BS13(S)C7	5.04 ± 0.18	4.88 ± 0.13	4.49 ± 0.13	5.74 ± 0.18	8.06 ± 0.17	8.71 ± 0.18
BS13(S)C8	5.08 ± 0.18	5.06 ± 0.13	4.78 ± 0.13	5.62 ± 0.18	8.03 ± 0.18	8.86 ± 0.17
BS13(S)C9	5.14 ± 0.16	4.94 ± 0.12	4.75 ± 0.12	5.63 ± 0.16	7.92 ± 0.16	8.70 ± 0.16
BS13(S)C10	5.07 ± 0.15	4.84 ± 0.13		6.13 ± 0.21	7.79 ± 0.19	8.95 ± 0.21
‡Regression coefficients						
BSSS(HT) b_1	0.18 ± 0.03	0.16 ± 0.04	0.18 ± 0.05	0.11 ± 0.03	0.11 ± 0.04	0.14 ± 0.04
BS13(S) b_0	4.94 ± 0.10	4.14 ± 0.12	3.737 ± 0.13	5.42 ± 0.10	7.58 ± 0.10	8.87 ± 0.10
BS13(S) b_1	0.01 ± 0.02	0.09 ± 0.02 q	0.124 ± 0.01 l	0.04 ± 0.02 l	0.04 ± 0.02 l	0.00 ± 0.02
Comparisons						
BSSS vs. BSSS(HT)C7	**	**	**	**	**	**
BSSS vs. BS13(S) b_0	**	**	**	**	**	**
BSSS(HT)C7 vs. BS13(S) b_0	ns	ns	ns	ns	ns	ns

l, q regression coefficients significant for linear and quadratic effects respectively at the 0.05 level of significance.

** statistical difference at the 0.01 level of significance. †Evaluation included only nine cycles of the S_2 progeny recurrent selection. ‡Estimates of the linear regression coefficients when fitting only the linear effect in the model. b_0 is the intercept at BS13(S)C0 and b_1 is the average response per cycle.

Table 4.5. Average response to selection per cycle for eight agronomic traits after ten cycles of S_2 progeny recurrent selection in the BS13(S) maize population.

	†Traits							
				Lodging		Height		Flowering Dates
Populations	‡Index	Stand	Grain Moisture	Root	Stalk	Ear	Plant	Silking
		plants ha^{-1} (X1000)	g kg^{-1}	----------%----------		----------cm----------		days after planting
Testcrosses				Outbred populations				
BS13(S) x TR7322	0.37 ± 0.29	0.03 ± 0.04	-0.1 ± 1.6 *c*	-0.1 ± 0.3	-0.4 ± 0.2	-1.2 ±0.4 *l*	-1.0 ± 0.4 *l*	-0.07 ± 0.05
BS13(S) x B97	1.04 ± 0.27 *l*	0.31 ± 0.41	-0.1 ± 0.3	-0.7 ± 0.3 *l*	-0.2 ± 0.2	-0.9 ± 0.4 *l*	-1.1 ± 0.4 *l*	-0.06 ± 0.05
BS13(S) x IA13	0.97 ± 0.29 *l*	0.22 ± 0.04	-0.5 ± 0.3 *c*	-0.7 ± 0.3 *l*	-0.2 ± 0.2	-1.0 ± 0.4 *l*	-0.9 ±0.4 *l*	-0.17 ± 0.05 *l*
Per se				F_{IS} = 0 populations				
BS13(S)	1.33 ± 0.27 *l*	0.09 ± 0.04 *l*	-1.0 ± 0.3 *l*	-0.8 ± 0.3 *l*	-0.8 ± 0.2 *l*	-3.0 ± 0.4 *l*	-3.0 ± 0.4 *l*	-0.19 ± 0.05 *l*
				F_{IS} = 0.5 populations				
BS13(S)	1.65 ± 0.23 *l*	0.24 ± 0.04 *l*	-1.1 ± 0.4 *c*	-0.5 ± 0.1 *l*	-0.3 ± 0.1 *c*	-1.9 ± 0.3 *l*	-2.1 ± 0.5 *q*	-0.27 ± 0.06 *l*
				¶F_{IS} = 0.75 populations				
BS13(S)	1.95 ± 0.24 *l*	0.37 ± 0.07 *l*	-0.8 ± 0.3 *q*	-0.5 ± 0.2 *q*	-0.3 ± 0.2 *q*	-1.6 ± 0.3 *l*	-1.5 ± 0.4 *c*	-0.22 ± 0.08 *l*

l, q, c regression coefficients significant for the linear, quadratic, and cubic responses respectively at the 0.05 level of significance.

†Estimate of the average response per cycle when fitting only the linear effect in the model. ‡Standardized relational-index computed from a ratio of average heritabilities of the selected trait to the average heritability for yield in each of the years of evaluation, multiplied by the observed values of the traits and summed across the selected traits; $I = quintles - (h^2 moisture/h^2 quintles)*moisture - (h^2 root\ loginding/h^2 quintles)*root\ lodging - (h^2 stalk\ lodging/h^2 quintles)*stalk\ logding.$

¶Evaluation included only nine cycles of S_2 progeny recurrent selection.

Table 4.6. Summary of the realized heritabilities for the four traits under selection in the BS13(S) maize population across ten cycles of selection. The heritabilities were computed as the mean of the selected trait regressed linearly on the cumulative selection differential at each cycle.

	Realized heritability (h_r^2) for populations per se or testcrossed					
	Inbreeding level of BS13(S) population			BS13(S) testcrosses		
	$F_{IS} = 0$	$F_{IS} = 0.5$	$F_{IS} = 0.75$	IA13	B97	TR7322
Grain Yield (t ha^{-1})	0.02 ± 0.02	0.10 ± 0.02**	0.12 ± 0.01**	0.04 ± 0.02*	0.04 ± 0.02*	0.00 ± 0.02
Grain Moisture (g kg^{-1})	-0.08 ± 0.01**	-0.08 ± 0.02**	-0.08 ± 0.02**	0.03 ± 0.01*	-0.02 ± 0.01	-0.03 ± 0.01*
Root Lodging (%)	-0.31 ± 0.10**	-0.18 ± 0.03**	-0.18 ± 0.07*	-0.29 ± 0.11*	-0.29 ± 0.10**	-0.02 ± 0.11
Stalk Lodging (%)	-0.32 ± 0.06**	-0.14 ± 0.04**	-0.19 ± 0.06**	-0.10 ± 0.07	-0.07 ± 0.06	-0.13 ± 0.06*

*,** regression coefficient significant at the 0.05 and 0.01 level respectively.

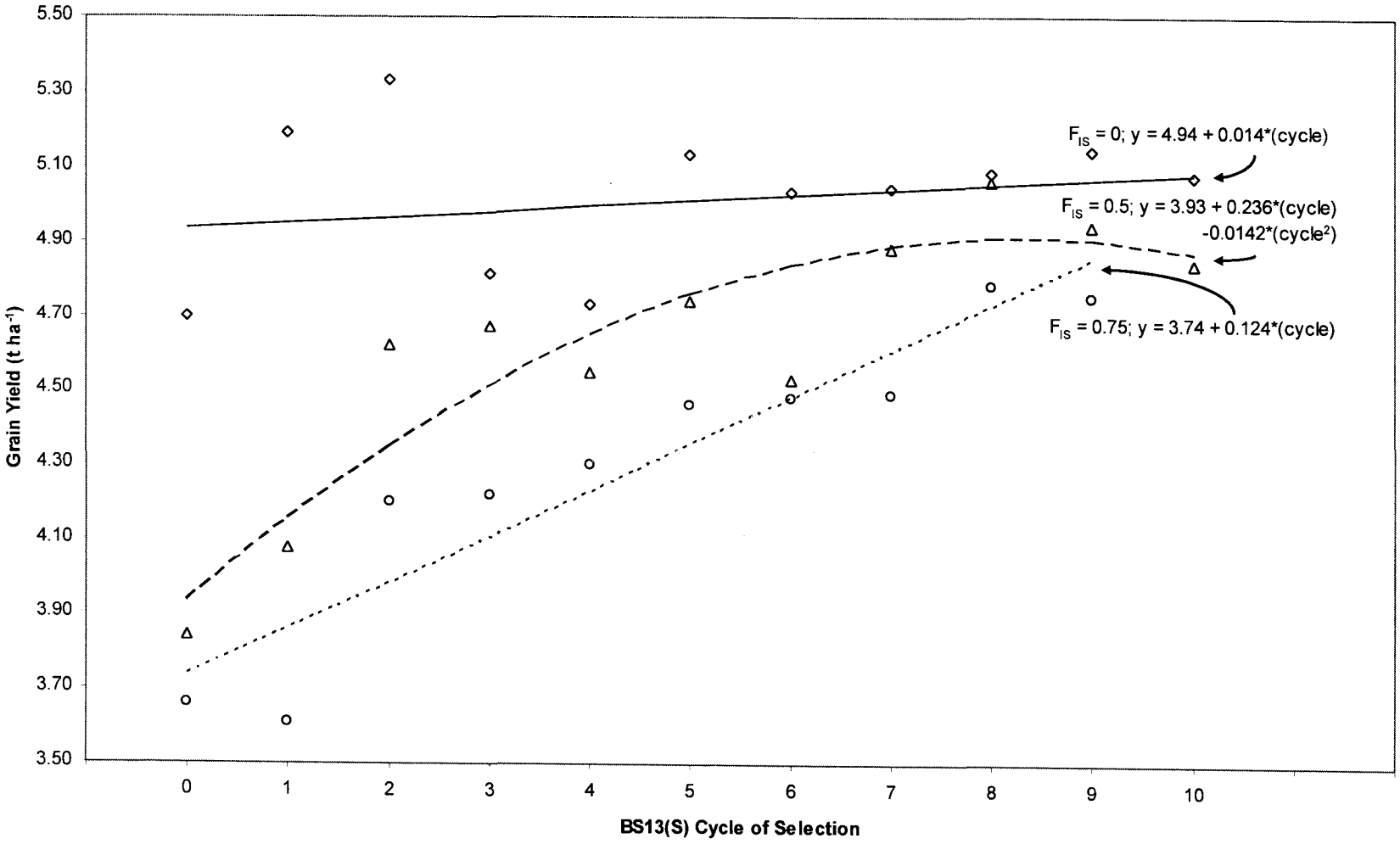


Figure 4.1. Observed values of BSSS, BSSS(HT)C7, and BS13(S) and predicted regressions of mean grain yields on 10 cycles of S_2 progeny recurrent selection in the BS13(S) maize population for S_0, S_1, and S_2 populations. Quadratic regression coefficients were significant for the $F_{IS} = 0.5$ and $F_{IS} = 0.75$ populations.

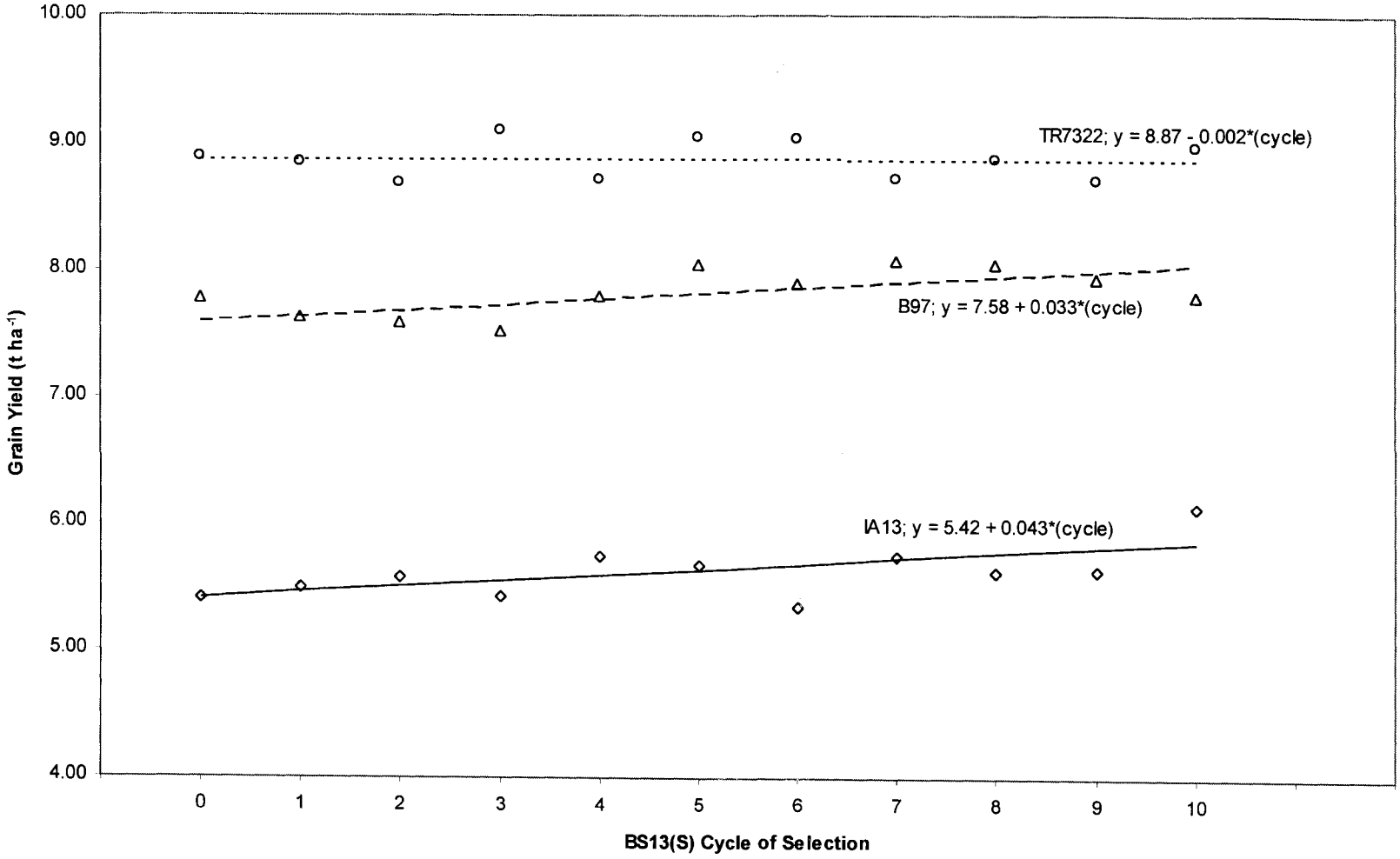


Figure 4.2. Observed values of BSSS, BSSS(HT)C7, and BS13(S) and predicted regressions of mean grain yields on 10 cycles of S_2 progeny recurrent selection in the BS13(S) maize population for testcrosses with TR7322, B97, and IA13. No regression coefficients were significant.

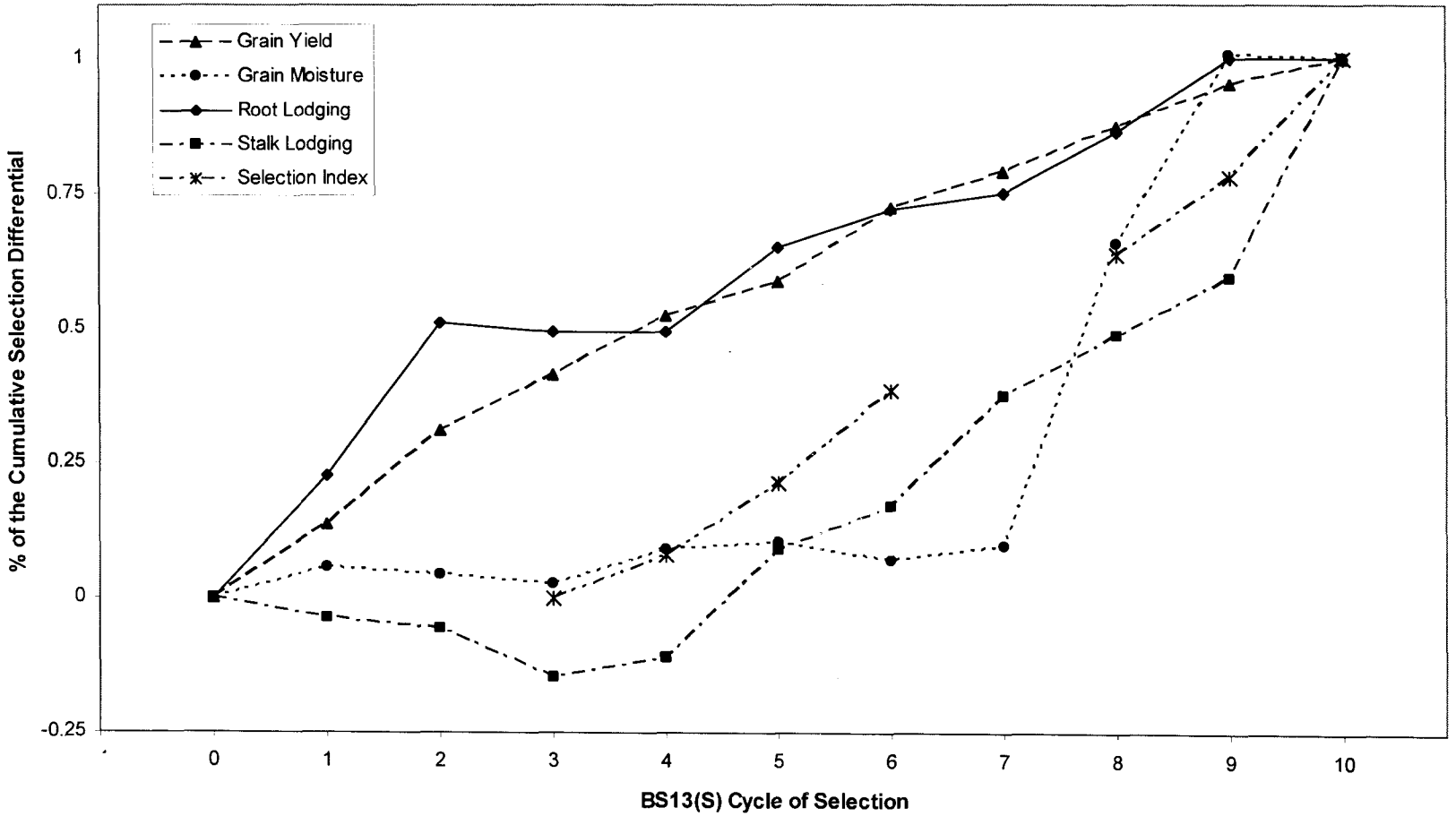


Figure 4.3. The cumulative selection differential for each trait under selection in BS13(S) maize population plotted at each cycle of selection on a percentage basis of cycle ten.

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Appendix A. Supplemental Tables

Supplemental Table A.4.1. Summary of mean grain moisture ± standard errors (se) for multiple response units of BSSS(HT) and BS13(S), linear regression coefficients, significance of linear, quadratic, and cubic effects, and tests of differences between populations.

	Populations per se response unit			Testcross response unit		
Population	F_{IS} = 0	F_{IS} = 0.5	F_{IS} = 0.75	IA13	B97	TR7322
	g kg^{-1}					
BSSS	181.4 ± 1.4	176.7 ± 1.9	181.2 ± 3.0	166.5 ± 1.6	165.1 ± 1.6	164.4 ± 1.5
BSSS(HT)C7	178.2 ± 1.5	178.2 ± 1.8	180.4 ± 2.9	172.1 ± 1.6	165.8 ± 1.6	167.6 ± 1.6
BS13(S)C0	178.2 ± 1.4	181.6 ± 1.5	178.7 ± 2.3	172.6 ± 1.6	166.0 ± 1.4	166.3 ± 1.5
BS13(S)C1	176.5 ± 1.7	173.4 ± 1.9	177.9 ± 2.9	170.8 ± 1.6	168.1 ± 1.5	166.8 ± 1.6
BS13(S)C2	179.4 ± 1.7	175.1 ± 1.8	174.0 ± 2.9	166.3 ± 1.6	169.8 ± 1.6	166.0 ± 1.6
BS13(S)C3	179.7 ± 1.6	180.1 ± 1.8	180.3 ± 2.8	169.3 ± 1.6	167.7 ± 1.6	166.5 ± 1.6
BS13(S)C4	180.9 ± 1.6	178.0 ± 1.8	178.5 ± 2.8	169.1 ± 1.6	168.9 ± 1.6	167.7 ± 1.6
BS13(S)C5	182.2 ± 1.7	179.1 ± 1.8	179.6 ± 2.8	169.1 ± 1.6	170.2 ± 1.6	170.3 ± 1.6
BS13(S)C6	181.3 ± 1.7	177.5 ± 1.8	177.6 ± 2.8	166.2 ± 1.6	169.8 ± 1.6	170.0 ± 1.6
BS13(S)C7	176.3 ± 1.6	175.6 ± 1.8	176.5 ± 2.8	168.8 ± 1.6	169.1 ± 1.6	169.4 ± 1.6
BS13(S)C8	175.7 ± 1.6	174.4 ± 1.8	170.9 ± 2.8	170.2 ± 1.7	166.8 ± 1.6	166.7 ± 1.6
BS13(S)C9	167.7 ± 1.5	167.6 ± 1.6	169.2 ± 2.6	166.6 ± 1.5	166.4 ± 1.5	163.5 ± 1.5
BS13(S)C10	167.7 ± 1.4	164.8 ± 1.8		163.5 ± 2.0	164.8 ± 1.8	162.7 ± 2.0
†Regression coefficients						
BSSS(HT) b_1	-0.33 ± 0.54	0.22 ± 0.79	-0.10 ± 0.77	0.48 ± 0.46	0.01 ± 0.52	0.51 ± 0.56
BS13(S) b_0	181.7 ± 1.6	180.6 ± 2.2	177.2 ± 1.7	170.8 ± 1.6	168.5 ± 1.5	167.7 ± 1.6
BS13(S) b_1	-1.0 ± 0.3 *l*	-1.1 ± 0.4 *c*	-0.8 ± 0.3 *q*	-0.5 ± 0.3 *c*	-0.1 ± 0.3	-0.1 ± 1.6 *c*
Comparisons						
BSSS vs. BSSS(HT)C7	ns	ns	ns	ns	ns	ns
BSSS vs. BS13(S) b_0	ns	ns	ns	ns	ns	ns
BSSS(HT)C7 vs. BS13(S) b_0	ns	ns	ns	ns	ns	ns

l, q, c regression coefficients significant for linear, quadratic, and cubic effects respectively at the 0.05 level of significance. ** statistical difference at the 0.01 level of significance. †Estimates of the linear regression coefficients when fitting only the linear effect in the model. b_0 is the intercept at BS13(S)C0 and b_1 is the average response per cycle.

Supplemental Table A.4.2. Summary of mean percentage of root lodging ± standard errors (se) for multiple response units of BSSS(HT) and BS13(S), linear regression coefficients, significance of linear, quadratic, and cubic effects, and tests of differences between populations.

	Populations per se response unit			Testcross response unit		
Population	F_{IS} = 0	F_{IS} = 0.5	F_{IS} = 0.75	1A13	B97	TR7322
	----------	----------	----------	%----------	----------	----------
BSSS	12.6 ± 2.5	5.6 ± 1.0	6.1 ± 1.5	20.5 ± 2.9	19.6 ± 2.8	5.8 ± 2.6
BSSS(HT)C7	14.6 ± 2.7	9.2 ± 1.0	5.5 ± 1.5	22.9 ± 2.8	25.0 ± 2.8	8.1 ± 2.8
BS13(S)C0	15.2 ± 2.5	8.0 ± 0.7	6.7 ± 1.2	22.4 ± 2.9	26.6 ± 2.5	7.3 ± 2.7
BS13(S)C1	13.1 ± 2.9	8.2 ± 1.0	9.9 ± 1.4	16.8 ± 2.8	22.0 ± 2.7	4.2 ± 2.8
BS13(S)C2	13.0 ± 2.8	6.5 ± 1.0	7.2 ± 1.4	21.3 ± 2.8	23.9 ± 2.8	5.9 ± 2.8
BS13(S)C3	12.1 ± 2.8	8.0 ± 1.0	7.2 ± 1.4	26.8 ± 2.8	27.6 ± 2.8	8.0 ± 2.8
BS13(S)C4	13.1 ± 2.8	5.8 ± 1.0	6.7 ± 1.4	22.6 ± 2.8	22.4 ± 2.8	6.0 ± 2.8
BS13(S)C5	9.6 ± 2.9	4.0 ± 1.0	6.9 ± 1.4	19.4 ± 2.8	23.4 ± 2.8	5.6 ± 2.8
BS13(S)C6	14.4 ± 2.8	5.0 ± 1.0	8.2 ± 1.4	17.8 ± 2.8	22.8 ± 2.8	4.6 ± 2.8
BS13(S)C7	9.4 ± 2.8	5.1 ± 1.0	4.9 ± 1.4	22.5 ± 2.8	18.7 ± 2.8	4.8 ± 2.8
BS13(S)C8	4.3 ± 2.8	4.5 ± 1.0	4.5 ± 1.4	18.1 ± 2.8	19.7 ± 2.8	6.2 ± 2.8
BS13(S)C9	5.1 ± 2.7	3.2 ± 0.8	1.6 ± 1.3	14.8 ± 2.7	16.9 ± 2.7	5.6 ± 2.7
BS13(S)C10	8.4 ± 2.6	3.9 ± 0.9		14.6 ± 3.6	14.8 ± 3.2	10.0 ± 3.6
†Regression coefficients						
BSSS(HT) b_1	0.04 ± 0.52	0.52 ± 0.21 l	-0.09 ± 0.34	0.46 ± 0.51	0.67 ± 0.55	0.11 ± 0.55
BS13(S) b_0	15.9 ± 1.5	8.0 ± 0.5	7.1 ± 1.0	23.3 ± 1.6	24.8 ± 1.5	7.0 ± 1.6
BS13(S) b_1	-0.8 ± 0.3 l	-0.5 ± 0.1 l	-0.5 ± 0.2 q	-0.7 ± 0.3 l	-0.7 ± 0.3 l	-0.1 ± 0.3
Comparisons						
BSSS vs. BSSS(HT)C7	ns	*	ns	ns	ns	ns
BSSS vs. BS13(S) b_0	ns	*	ns	ns	ns	ns
BSSS(HT)C7 vs. BS13(S) b_0	ns	ns	ns	ns	ns	ns

l, q regression coefficients significant for linear and quadratic effects respectively at the 0.05 level of significance.

** statistical difference at the 0.01 level of significance. †Estimates of the linear regression coefficients when fitting only the linear effect in the model. b_0 is the intercept at BS13(S)C0 and b_1 is the average response per cycle.

Supplemental Table A.4.3. Summary of mean percentage of stalk lodging ± standard errors (se) for multiple response units of BSSS(HT) and BS13(S), linear regression coefficients, significance of linear, quadratic, and cubic effects, and tests of differences between populations.

	Populations per se response unit			Testcross response unit		
Population	$F_{IS} = 0$	$F_{IS} = 0.5$	$F_{IS} = 0.75$	IA13	B97	TR7322
	----------	----------	----------	%	----------	----------
BSSS	12.4 ± 1.4	8.6 ± 1.2	8.4 ± 1.4	22.4 ± 1.6	14.1 ± 1.7	11.1 ± 1.5
BSSS(HT)C7	11.1 ± 1.5	7.1 ± 1.2	6.6 ± 1.4	17.5 ± 1.7	12.4 ± 1.7	7.6 ± 1.7
BS13(S)C0	12.8 ± 1.4	8.2 ± 0.9	7.9 ± 1.1	22.0 ± 1.6	11.2 ± 1.4	8.1 ± 1.5
BS13(S)C1	19.0 ± 1.7	10.2 ± 1.2	10.0 ± 1.4	19.2 ± 1.6	10.7 ± 1.5	11.5 ± 1.6
BS13(S)C2	17.8 ± 1.7	9.4 ± 1.2	10.5 ± 1.4	25.6 ± 1.7	9.9 ± 1.7	10.9 ± 1.7
BS13(S)C3	16.7 ± 1.7	10.3 ± 1.2	10.3 ± 1.3	21.3 ± 1.7	10.6 ± 1.7	9.7 ± 1.7
BS13(S)C4	19.0 ± 1.7	11.0 ± 1.2	11.8 ± 1.3	23.6 ± 1.7	12.6 ± 1.7	9.1 ± 1.7
BS13(S)C5	16.2 ± 1.7	8.3 ± 1.2	7.6 ± 1.3	24.5 ± 1.7	9.3 ± 1.7	9.8 ± 1.7
BS13(S)C6	15.3 ± 1.7	10.5 ± 1.2	9.0 ± 1.3	25.9 ± 1.7	11.1 ± 1.7	7.8 ± 1.7
BS13(S)C7	12.0 ± 1.7	7.0 ± 1.2	7.5 ± 1.3	21.1 ± 1.7	9.0 ± 1.7	7.0 ± 1.7
BS13(S)C8	11.4 ± 1.7	5.8 ± 1.2	6.6 ± 1.3	23.1 ± 1.7	9.6 ± 1.7	8.6 ± 1.6
BS13(S)C9	12.1 ± 1.6	6.4 ± 1.0	7.4 ± 1.2	20.8 ± 1.5	7.5 ± 1.5	6.6 ± 1.5
BS13(S)C10	7.6 ± 1.4	6.8 ± 1.1		16.1 ± 2.0	9.7 ± 1.8	6.0 ± 2.0
†Regression coefficients						
BSSS(HT) b_1	-0.03 ± 0.40	-0.22 ± 0.32	-0.26 ± 0.32	-0.90 ± 0.39 *l*	-0.53 ± 0.42	-0.35 ± 0.43
BS13(S) b_0	18.3 ± 1.2	10.2 ± 0.8	8.8 ± 0.9	22.6 ± 1.2	11.6 ± 1.2	10.0 ± 1.2
BS13(S) b_1	-0.8 ± 0.2 *l*	-0.3 ± 0.1 *c*	-0.3 ± 0.2 *q*	-0.2 ± 0.2	-0.2 ± 0.2	-0.4 ± 0.2
Comparisons						
BSSS vs. BSSS(HT)C7	*	ns	ns	ns	ns	ns
BSSS vs. BS13(S) b_0	*	ns	ns	ns	ns	ns
BSSS(HT)C7 vs. BS13(S) b_0	ns	ns	*	ns	ns	ns

l, q, c regression coefficients significant for linear, quadratic, and cubic effects respectively at the 0.05 level of significance. ** statistical difference at the 0.01 level of significance. †Estimates of the linear regression coefficients when fitting only the linear effect in the model. b_0 is the intercept at BS13(S)C0 and b_1 is the average response per cycle.

Supplemental Table A.4.4. Summary of mean plant height ± standard errors (se) for multiple response units of BSSS(HT) and BS13(S), linear regression coefficients, significance of linear, quadratic, and cubic effects, and tests of differences between populations.

	Populations per se response unit			Testcross response unit		
	S_0	S_1	S_2	IA13	B97	TR7322
Population	----------	----------	----------	cm ----------	----------	----------
BSSS	241.3 ± 1.6	195.8 ± 1.7	195.4 ± 2.0	260.2 ± 2.1	251.7 ± 3.7	244.1 ± 1.8
BSSS(HT)C7	232.7 ± 1.7	199.2 ± 1.7	192.0 ± 2.0	260.7 ± 1.9	255.1 ± 3.8	246.9 ± 1.9
BS13(S)C0	230.2 ± 1.6	196.5 ± 1.4	191.0 ± 1.6	262.3 ± 2.1	256.0 ± 3.1	248.3 ± 1.8
BS13(S)C1	224.5 ± 1.9	193.4 ± 1.8	185.2 ± 2.0	259.5 ± 1.9	252.3 ± 3.6	247.3 ± 1.8
BS13(S)C2	221.0 ± 1.9	186.3 ± 1.7	184.0 ± 2.0	257.1 ± 1.9	250.5 ± 3.9	241.4 ± 1.9
BS13(S)C3	224.5 ± 1.9	189.9 ± 1.7	190.6 ± 1.9	264.5 ± 2.0	251.1 ± 3.8	247.2 ± 1.9
BS13(S)C4	223.7 ± 1.9	191.8 ± 1.7	186.0 ± 2.0	259.5 ± 1.9	254.6 ± 3.9	245.8 ± 1.9
BS13(S)C5	226.8 ± 1.9	194.9 ± 1.7	187.1 ± 1.9	261.8 ± 1.9	252.8 ± 3.9	248.9 ± 1.9
BS13(S)C6	228.7 ± 1.9	192.9 ± 1.8	186.5 ± 2.0	260.9 ± 1.9	255.6 ± 3.8	246.6 ± 1.9
BS13(S)C7	211.5 ± 1.9	182.4 ± 1.7	179.7 ± 2.0	253.5 ± 2.0	245.0 ± 3.8	241.5 ± 1.9
BS13(S)C8	204.8 ± 1.9	179.9 ± 1.7	177.7 ± 2.0	254.3 ± 1.9	246.1 ± 3.8	238.4 ± 1.8
BS13(S)C9	198.2 ± 1.7	174.5 ± 1.5	172.8 ± 1.7	249.8 ± 1.7	243.2 ± 3.3	237.4 ± 1.7
BS13(S)C10	197.9 ± 1.6	171.4 ± 1.9	161.3 ± 3.6	252.2 ± 3.1	242.5 ± 4.7	235.4 ± 3.1
†Regression coefficients						
BSSS(HT) b_1	-1.06 ± 0.90	0.49 ± 1.02	-0.49 ± 0.95	-0.26 ± 0.69	0.20 ± 0.82	0.70 ± 0.91
BS13(S) b_0	232.4 ± 2.5	197.3 ± 2.8	189.6 ± 2.2	261.3 ± 2.6	254.6 ± 2.4	247.1 ± 2.6
BS13(S) b_1	-3.0 ± 0.4 *l*	-2.1 ± 0.5 *q*	-1.5 ± 0.4 *c*	-0.9 ± 0.4 *l*	-1.1 ± 0.4 *l*	-1.0 ± 0.4 *l*
Comparisons						
BSSS vs. BSSS(HT)C7	ns	ns	ns	ns	ns	ns
BSSS vs. BS13(S) b_0	ns	ns	ns	ns	ns	ns
BSSS(HT)C7 vs. BS13(S) b_0	ns	ns	ns	ns	ns	ns

l, q, c regression coefficients significant for linear, quadratic, and cubic effects respectively at the 0.05 level of significance. ** statistical difference at the 0.01 level of significance. †Estimates of the linear regression coefficients when fitting only the linear effect in the model. b_0 is the intercept at BS13(S)C0 and b_1 is the average response per cycle.

Supplemental Table A.4.5. Summary of mean ear height ± standard errors (se) for multiple response units of BSSS(HT) and BS13(S), linear regression coefficients, significance of linear, quadratic, and cubic effects, and tests of differences between populations.

	Populations per se response unit			Testcross response unit		
Population	$F_{IS} = 0$	$F_{IS} = 0.5$	$F_{IS} = 0.75$	IA13	B97	TR7322
	cm					
BSSS	127.1 ± 1.4	98.3 ± 1.5	98.3 ± 1.7	144.8 ± 1.8	121.3 ± 1.6	118.6 ± 3.0
BSSS(HT)C7	120.0 ± 1.5	99.4 ± 1.5	92.7 ± 1.7	142.0 ± 1.7	123.8 ± 1.7	122.4 ± 3.2
BS13(S)C0	118.9 ± 1.4	98.4 ± 1.2	95.3 ± 1.5	142.0 ± 1.8	122.8 ± 1.4	120.1 ± 3.1
BS13(S)C1	118.2 ± 1.7	97.7 ± 1.5	92.7 ± 1.8	143.0 ± 1.6	123.0 ± 1.6	123.1 ± 3.0
BS13(S)C2	110.9 ± 1.6	88.2 ± 1.5	87.3 ± 1.7	140.2 ± 1.7	119.8 ± 1.7	117.7 ± 3.2
BS13(S)C3	118.4 ± 1.6	96.0 ± 1.5	93.3 ± 1.7	145.7 ± 1.7	121.9 ± 1.7	124.4 ± 3.2
BS13(S)C4	117.5 ± 1.6	93.4 ± 1.5	89.7 ± 1.7	142.5 ± 1.7	122.2 ± 1.7	121.4 ± 3.2
BS13(S)C5	116.7 ± 1.7	93.4 ± 1.5	88.3 ± 1.7	143.8 ± 1.7	118.2 ± 1.7	121.2 ± 3.2
BS13(S)C6	115.6 ± 1.6	92.9 ± 1.5	88.9 ± 1.7	144.7 ± 1.7	122.3 ± 1.7	120.2 ± 3.2
BS13(S)C7	105.3 ± 1.6	86.9 ± 1.5	82.7 ± 1.7	135.8 ± 1.7	114.2 ± 1.7	115.9 ± 3.2
BS13(S)C8	96.5 ± 1.6	83.1 ± 1.5	81.8 ± 1.7	135.8 ± 1.7	114.9 ± 1.7	113.1 ± 3.0
BS13(S)C9	91.8 ± 1.5	79.0 ± 1.3	79.0 ± 1.5	132.0 ± 1.5	112.4 ± 1.5	111.9 ± 2.9
BS13(S)C10	90.0 ± 1.4	77.2 ± 1.7		133.1 ± 2.8	113.6 ± 2.1	110.0 ± 5.4
†Regression coefficients						
BSSS(HT) b_1	-0.92 ± 0.82	0.16 ± 0.74	-0.82 ± 0.71	-0.02 ± 0.63	-0.01 ± 0.74	0.89 ± 0.84
BS13(S) b_0	124.0 ± 2.3	99.4 ± 2.1	95.1 ± 1.4	144.7 ± 2.4	122.8 2.2	123.4 ± 2.4
BS13(S) b_1	-3.0 ± 0.4 ƒ	-1.9 ± 0.3 ƒ	-1.6 ± 0.3 ƒ	-1.0 ± 0.4 ƒ	-0.9 0.4 ƒ	-1.2 ± 0.4 ƒ
Comparisons						
BSSS vs. BSSS(HT)C7	ns	ns	ns	ns	ns	ns
BSSS vs. BS13(S) b_0	ns	ns	ns	ns	ns	ns
BSSS(HT)C7 vs. BS13(S) b_0	ns	ns	ns	ns	ns	ns

ƒ regression coefficients significant for linear effects at the 0.05 level of significance. ** statistical difference at the 0.01 level of significance. †Estimates of the linear regression coefficients when fitting only the linear effect in the model. b_0 is the intercept at BS13(S)C0 and b_1 is the average response per cycle.

Supplemental Table A.4.6. Summary of mean silking date ± standard errors (se) for multiple response units of BSSS(HT) and BS13(S), linear regression coefficients, significance of linear, quadratic, and cubic effects, and tests of differences between populations.

	Populations per se response unit			Testcross response unit		
Population	$F_{IS} = 0$	$F_{IS} = 0.5$	$F_{IS} = 0.75$	IA13	B97	TR7322
	----------days after planting----------					
BSSS	79.31 ± 0.50	81.17 ± 0.57	74.67 ± 0.70	78.11 ± 0.72	76.69 ± 0.58	76.31 ± 1.08
BSSS(HT)C7	77.78 ± 0.51	79.33 ± 0.57	75.33 ± 0.70	76.86 ± 0.58	76.96 ± 0.58	75.80 ± 1.17
BS13(S)C0	78.78 ± 0.51	79.75 ± 0.54	75.67 ± 0.50	77.38 ± 0.72	76.22 ± 0.51	75.57 ± 1.08
BS13(S)C1	77.23 ± 0.58	78.50 ± 0.57	74.67 ± 0.70	77.80 ± 0.54	75.68 ± 0.54	75.60 ± 1.08
BS13(S)C2	77.31 ± 0.58	78.17 ± 0.57	74.33 ± 0.70	76.34 ± 0.58	76.79 ± 0.58	75.00 ± 1.17
BS13(S)C3	78.11 ± 0.58	79.17 ± 0.57	74.00 ± 0.70	76.65 ± 0.58	76.34 ± 0.58	75.02 ± 1.17
BS13(S)C4	76.85 ± 0.58	78.00 ± 0.57	74.33 ± 0.70	76.80 ± 0.58	76.44 ± 0.58	75.37 ± 1.17
BS13(S)C5	77.38 ± 0.58	78.00 ± 0.57	73.33 ± 0.70	76.35 ± 0.58	76.40 ± 0.58	75.29 ± 1.17
BS13(S)C6	77.77 ± 0.58	79.00 ± 0.57	75.33 ± 0.70	77.08 ± 0.58	75.78 ± 0.58	75.58 ± 1.17
BS13(S)C7	76.82 ± 0.58	77.33 ± 0.57	74.33 ± 0.70	76.67 ± 0.58	76.43 ± 0.58	74.37 ± 1.17
BS13(S)C8	76.44 ± 0.58	77.17 ± 0.57	73.00 ± 0.70	75.67 ± 0.58	75.98 ± 0.58	74.51 ± 1.09
BS13(S)C9	75.86 ± 0.58	76.23 ± 0.55	73.00 ± 0.70	76.32 ± 0.54	75.91 ± 0.54	75.25 ± 1.17
BS13(S)C10	76.37 ± 0.51	76.82 ± 0.78		75.73 ± 0.72	75.38 ± 0.54	75.25 ± 1.43
†Regression coefficients						
BSSS(HT) b_1	-0.19 ± 0.09 ƒ	-0.26 ± 0.13 ƒ	0.10 ± 0.14	-0.20 ± 0.12	0.02 ± 0.11	-0.08 ± 0.10
BS13(S) b_0	78.12 ± 0.28	79.37 ± 0.36	75.21 ± 0.39	77.52 ± 0.31	76.48 ± 0.27	75.46 ± 0.28
BS13(S) b_1	-0.19 ± 0.05 ƒ	-0.27 ± 0.06 ƒ	-0.22 ± 0.08 ƒ	-0.17 ± 0.05 ƒ	-0.06 ± 0.05	-0.07 ± 0.05
Comparisons						
BSSS vs. BSSS(HT)C7	*	*	ns	ns	ns	ns
BSSS vs. BS13(S) b_0	*	*	ns	ns	ns	*
BSSS(HT)C7 vs. BS13(S) b_0	ns	ns	ns	ns	ns	ns

ƒ regression coefficients significant for linear effects at the 0.05 level of significance. ** statistical difference at the 0.01 level of significance. †Estimates of the linear regression coefficients when fitting only the linear effect in the model. b_0 is the intercept at BS13(S)C0 and b_1 is the average response per cycle.

Supplemental Table A.4.7. Summary of mean index ± standard errors (se) for multiple response units of BSSS(HT) and BS13(S), linear regression coefficients, significance of linear, quadratic, and cubic effects, and tests of differences between populations.

	Population response units			Testcross response units		
Population	$F_{IS} = 0$	$F_{IS} = 0.5$	$F_{IS} = 0.75$	IA13	B97	TR7322
	†index					
BSSS	-1.32 ± 2.54	-0.52 ± 1.60	-4.57 ± 2.06	-1.48 ± 2.89	25.87 ± 2.90	48.41 ± 5.25
BSSS(HT)C7	12.46 ± 2.66	10.02 ± 1.54	9.51 ± 1.96	10.22 ± 2.90	36.18 ± 2.93	58.19 ± 5.65
BS13(S)C0	9.71 ± 2.52	8.35 ± 1.25	6.74 ± 1.62	5.70 ± 2.92	34.43 ± 2.51	59.68 ± 5.27
BS13(S)C1	11.21 ± 2.98	9.80 ± 1.59	2.86 ± 1.96	12.87 ± 2.86	37.30 ± 2.67	58.24 ± 5.54
BS13(S)C2	14.52 ± 2.94	16.69 ± 1.54	10.78 ± 1.96	5.25 ± 2.88	36.46 ± 2.88	56.69 ± 5.65
BS13(S)C3	9.65 ± 2.90	15.33 ± 1.53	10.80 ± 1.90	6.14 ± 2.88	32.94 ± 2.88	60.11 ± 5.65
BS13(S)C4	7.04 ± 2.91	14.72 ± 1.53	10.57 ± 1.91	8.14 ± 2.90	36.08 ± 2.91	60.16 ± 5.68
BS13(S)C5	15.63 ± 2.95	20.48 ± 1.56	14.84 ± 1.89	9.85 ± 2.91	41.00 ± 2.90	60.09 ± 5.68
BS13(S)C6	11.13 ± 2.94	15.75 ± 1.56	13.80 ± 1.90	5.10 ± 2.90	38.34 ± 2.88	62.53 ± 5.73
BS13(S)C7	18.25 ± 2.93	22.33 ± 1.55	16.83 ± 1.91	10.75 ± 2.88	44.03 ± 2.88	61.51 ± 5.68
BS13(S)C8	21.84 ± 2.90	25.34 ± 1.55	21.91 ± 1.91	10.69 ± 2.93	43.42 ± 2.91	59.07 ± 5.54
BS13(S)C9	22.23 ± 2.77	25.58 ± 1.37	23.27 ± 1.77	14.61 ± 2.68	44.94 ± 2.67	61.66 ± 5.35
BS13(S)C10	23.19 ± 2.53	23.68 ± 1.50	15.77 ± 2.13	22.73 ± 3.55	44.44 ± 3.21	61.15 ± 6.94
‡Regression coefficients						
BSSS(HT) b_1	1.92 ± 0.54 ƒ	1.50 ± 0.51 ƒ	1.99 0.62 ƒ	1.43 ± 0.55 ƒ	1.36 ± 0.59 ƒ	1.59 ± 0.58 ƒ
BS13(S) b_0	6.38 ± 1.60	9.73 ± 1.38	4.58 ± 1.28	5.32 ± 1.69	34.23 ± 1.57	58.43 ± 1.65
BS13(S) b_1	1.33 ± 0.27 ƒ	1.65 ± 0.23 ƒ	1.95 ± 0.24 ƒ	0.97 ± 0.29 ƒ	1.04 ± 0.27 ƒ	0.37 ± 0.29
Comparisons						
BSSS vs. BSSS(HT)C7	**	**	**	*	*	**
BSSS vs. BS13(S) b_0	*	**	**	ns	*	**
BSSS(HT)C7 vs. BS13(S) b_0	ns	ns	ns	ns	ns	ns

ƒ regression coefficients significant for linear effects at the 0.05 level of significance. ** statistical difference at the 0.01 level of significance.

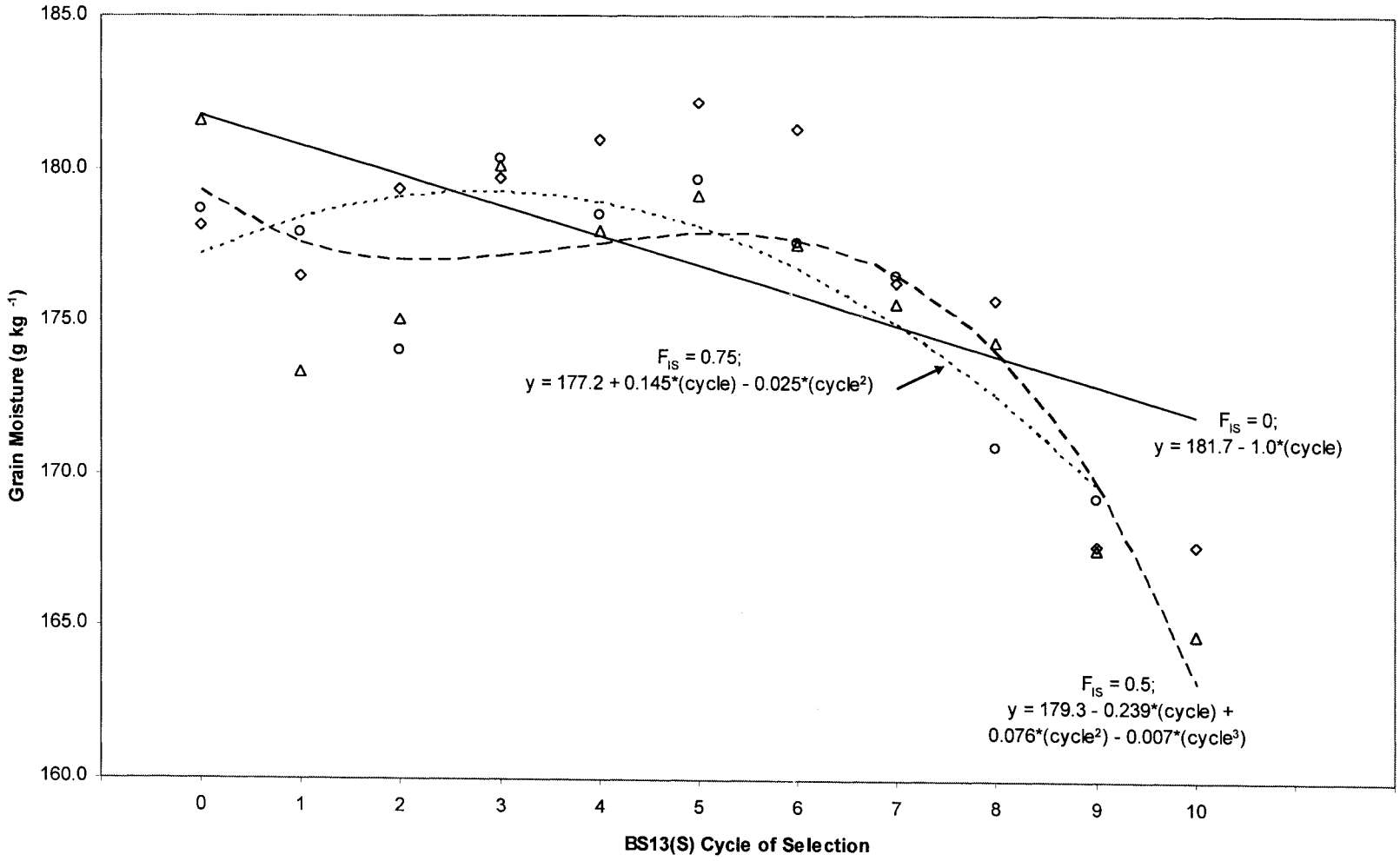
†Proportional summation-index computed from an average of the heritabilities for the traits under selection, as computed in each of the years of advancement evaluation, proportionally to yield heritability multiplied by the observed values of the traits; $I = quintles - (h^2 moisture/h^2 quintles)*moisture - (h^2 root\ loginding/h^2 quintles)*root\ lodging - (h^2 stalk\ lodging/h^2 quintles)*stalk\ logding$. ‡Estimates of the linear regression coefficients when fitting only the linear effect in the model. b_0 is the intercept at BS13(S)C0 and b_1 is the average response per cycle.

Supplemental Table A.4.8. Summary of mean plant density ± SE for multiple response units of BSSS(HT) and BS13(S), linear regression coefficients, significance of linear, quadratic, and cubic effects, and tests of differences between populations.

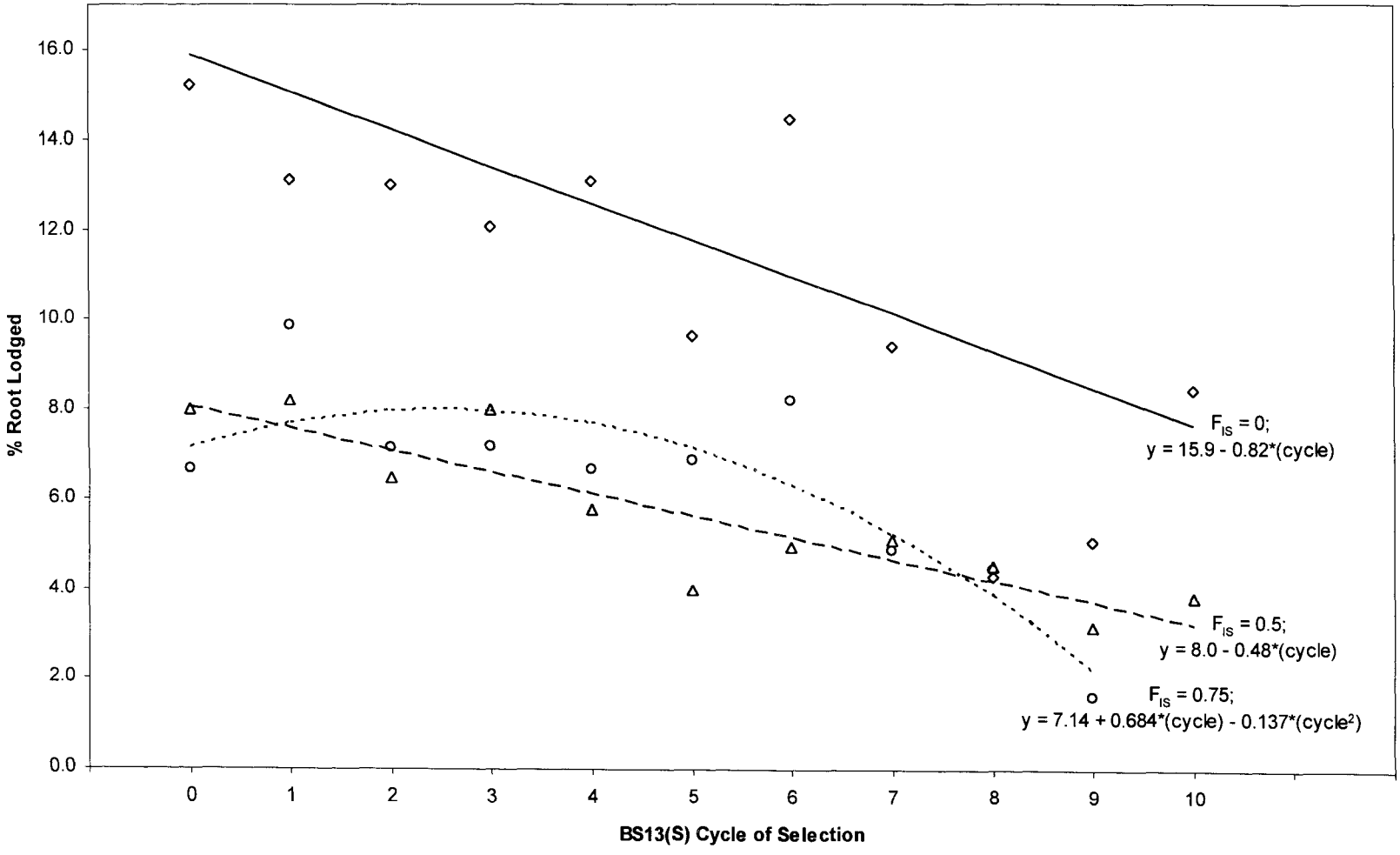
	Populations per se response units			Testcross response units		
Population	$F_{IS} = 0$	$F_{IS} = 0.5$	$F_{IS} = 0.75$	IA13	B97	TR7322
	----------plants ha^{-1} (X 1000)----------					
BSSS	63.75 ± 0.39	62.12 ± 0.54	60.32 ± 0.72	64.88 ± 0.45	64.63 ± 0.47	65.54 ± 0.42
BSSS(HT)C7	64.02 ± 0.42	62.09 ± 0.53	59.26 ± 0.71	64.09 ± 0.47	65.72 ± 0.47	65.26 ± 0.47
BS13(S)C0	63.59 ± 0.39	61.41 ± 0.40	59.11 ± 0.58	64.89 ± 0.46	65.56 ± 0.38	64.93 ± 0.42
BS13(S)C1	62.98 ± 0.49	61.38 ± 0.54	59.46 ± 0.71	65.45 ± 0.46	66.01 ± 0.42	65.60 ± 0.46
BS13(S)C2	63.71 ± 0.48	61.50 ± 0.53	60.22 ± 0.70	64.87 ± 0.47	65.61 ± 0.47	66.36 ± 0.47
BS13(S)C3	64.51 ± 0.47	61.98 ± 0.53	60.91 ± 0.69	65.39 ± 0.47	65.04 ± 0.47	65.74 ± 0.47
BS13(S)C4	65.25 ± 0.47	62.43 ± 0.53	61.20 ± 0.69	65.77 ± 0.47	65.45 ± 0.47	65.96 ± 0.47
BS13(S)C5	64.76 ± 0.48	63.63 ± 0.54	61.70 ± 0.69	65.82 ± 0.47	65.71 ± 0.47	65.16 ± 0.47
BS13(S)C6	63.76 ± 0.48	63.18 ± 0.54	61.26 ± 0.69	66.60 ± 0.47	66.10 ± 0.47	65.73 ± 0.48
BS13(S)C7	64.11 ± 0.48	63.20 ± 0.53	62.10 ± 0.70	65.44 ± 0.47	66.41 ± 0.47	65.69 ± 0.47
BS13(S)C8	64.26 ± 0.47	63.66 ± 0.53	62.76 ± 0.70	66.84 ± 0.48	65.71 ± 0.47	65.89 ± 0.45
BS13(S)C9	64.47 ± 0.44	63.00 ± 0.45	62.14 ± 0.64	66.63 ± 0.42	65.57 ± 0.42	65.78 ± 0.43
BS13(S)C10	64.48 ± 0.39	63.62 ± 0.49		67.20 ± 0.56	66.14 ± 0.51	65.71 ± 0.55
†Regression coefficients						
BSSS(HT) b_1	0.04 ± 0.08	0.00 ± 0.11	-0.15 ± 0.14	-0.04 ± 0.09	0.17 ± 0.09	-0.02 ± 0.09
BS13(S) b_0	63.76 ± 0.24	61.42 ± 0.27	59.40 ± 0.37	64.80 ± 0.26	65.59 ± 0.24	65.56 ± 0.25
BS13(S) b_1	0.09 ± 0.04 ƒ	0.24 ± 0.04 ƒ	0.37 ± 0.07 ƒ	0.22 ± 0.04	0.31 ± 0.41	0.03 ± 0.04
Comparisons						
BSSS vs. BSSS(HT)C7	ns	ns	ns	ns	ns	ns
BSSS vs. BS13(S) b_0	ns	ns	ns	ns	*	ns
BSSS(HT)C7 vs. BS13(S) b_0	ns	ns	ns	ns	ns	ns

ƒ regression coefficients significant for linear effects at the 0.05 level of significance. ** statistical difference at the 0.01 level of significance. †Estimates of the linear regression coefficients when fitting only the linear effect in the model. b_0 is the intercept at BS13(S)C0 and b_1 is the average response per cycle.

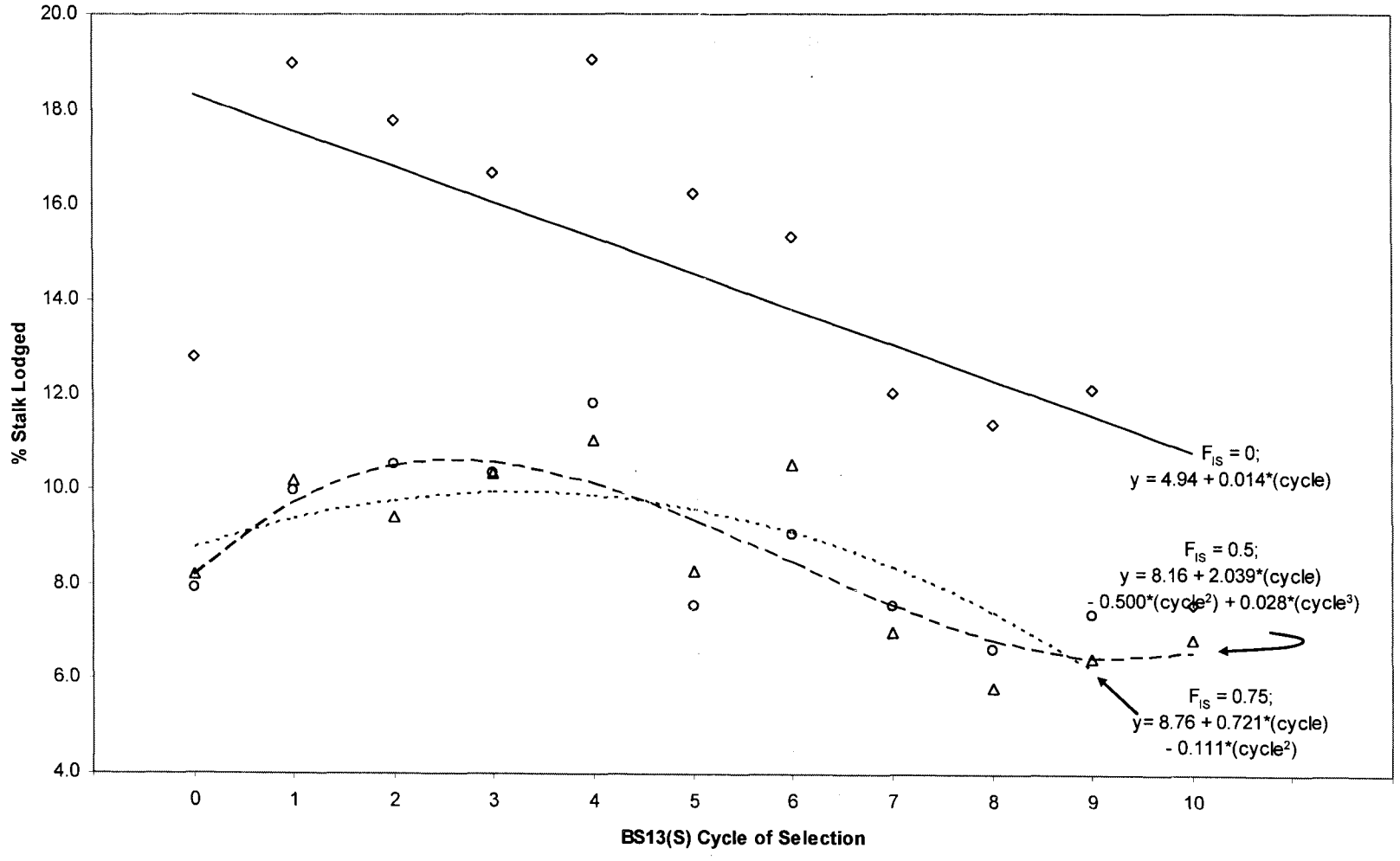
Appendix B. Supplemental Figures



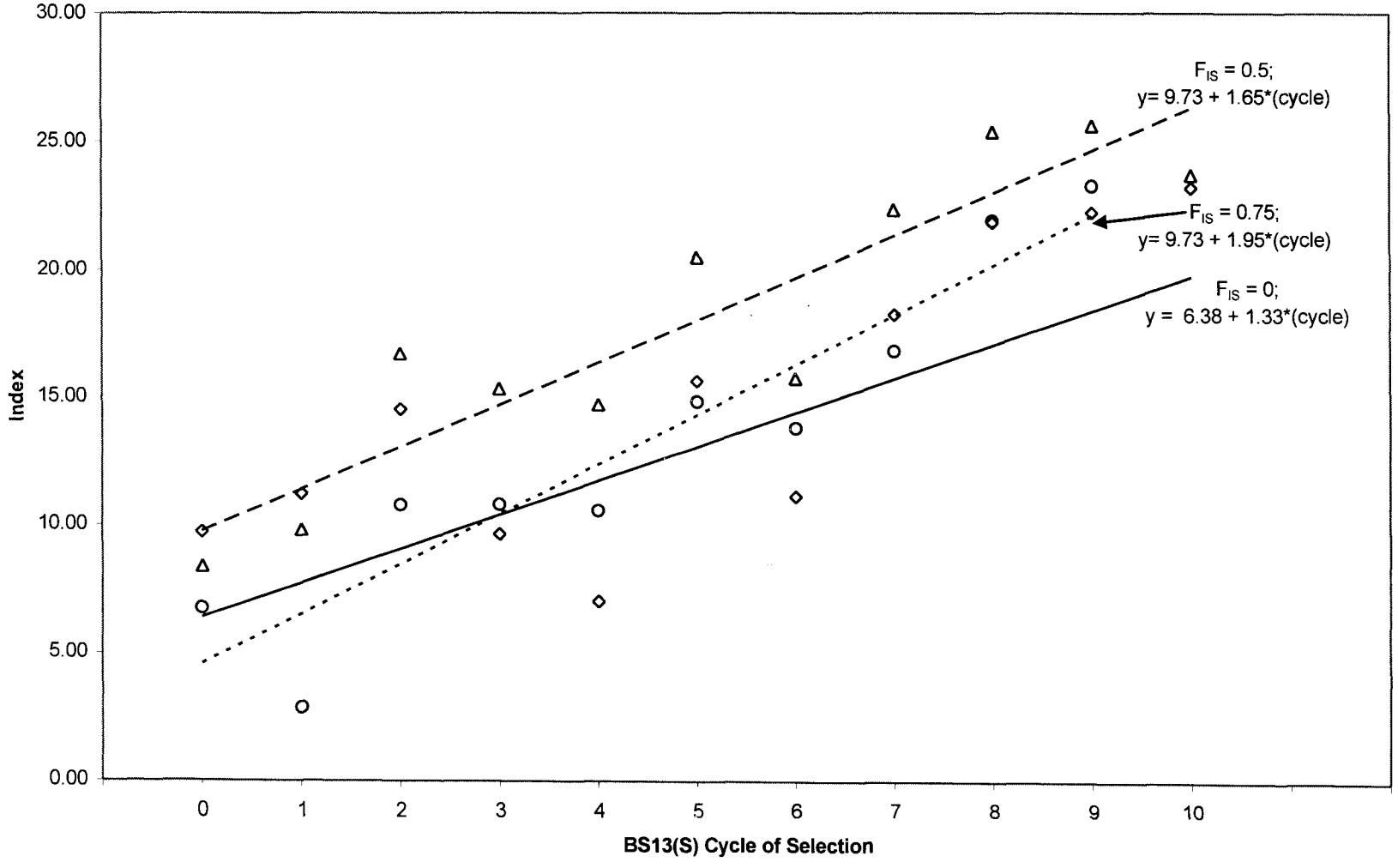
Supplemental Figure B.4.1. Observed values of BSSS, BSSS(HT)C7, and BS13(S) and predicted regressions of mean grain moisture on 10 cycles of S_2 progeny recurrent selection in the BS13(S) maize population for $F_{IS} = 0$, $F_{IS} = 0.5$, and $F_{IS} = 0.75$ populations.



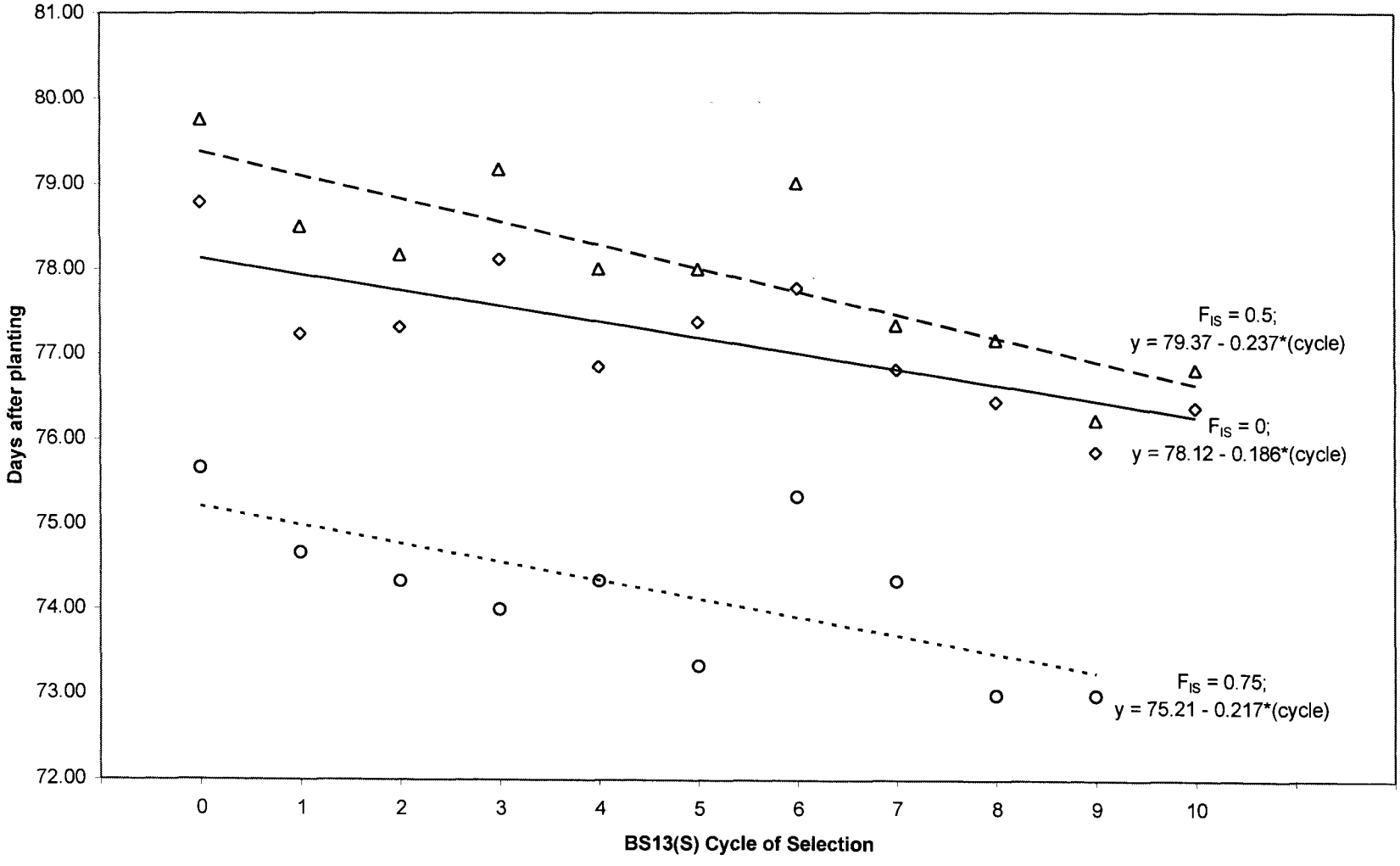
Supplemental Figure B.4.2. Observed values of BSSS, BSSS(HT)C7, and BS13(S) and predicted regressions of mean root lodging on 10 cycles of S_2 progeny recurrent selection in the BS13(S) maize population for $F_{IS} = 0$, $F_{IS} = 0.5$, and $F_{IS} = 0.75$ populations.



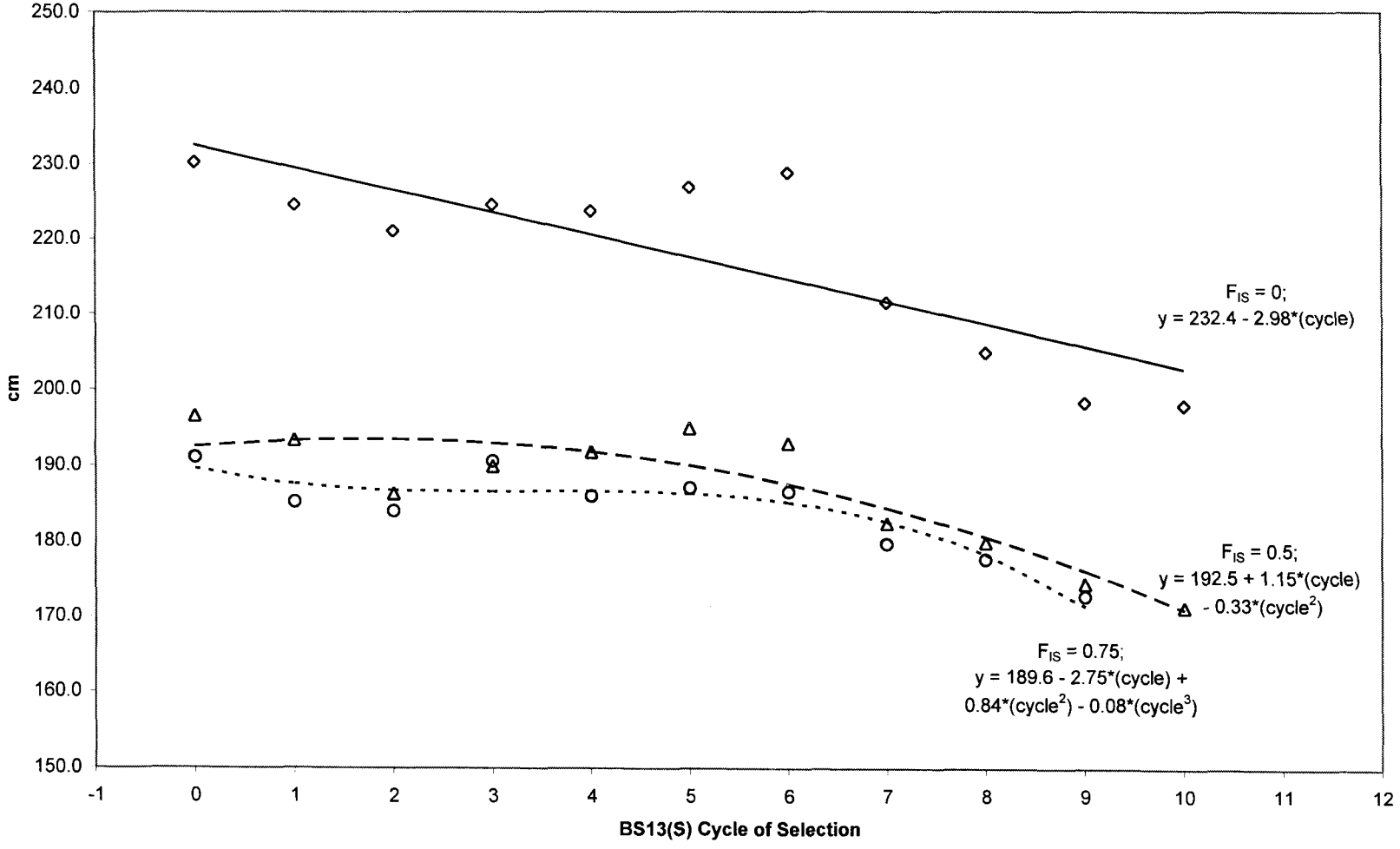
Supplemental Figure B.4.3. Observed values of BSSS, BSSS(HT)C7, and BS13(S) and predicted regressions of mean stalk lodging on 10 cycles of S_2 progeny recurrent selection in the BS13(S) maize population for $F_{IS} = 0$, $F_{IS} = 0.5$, and $F_{IS} = 0.75$ populations.



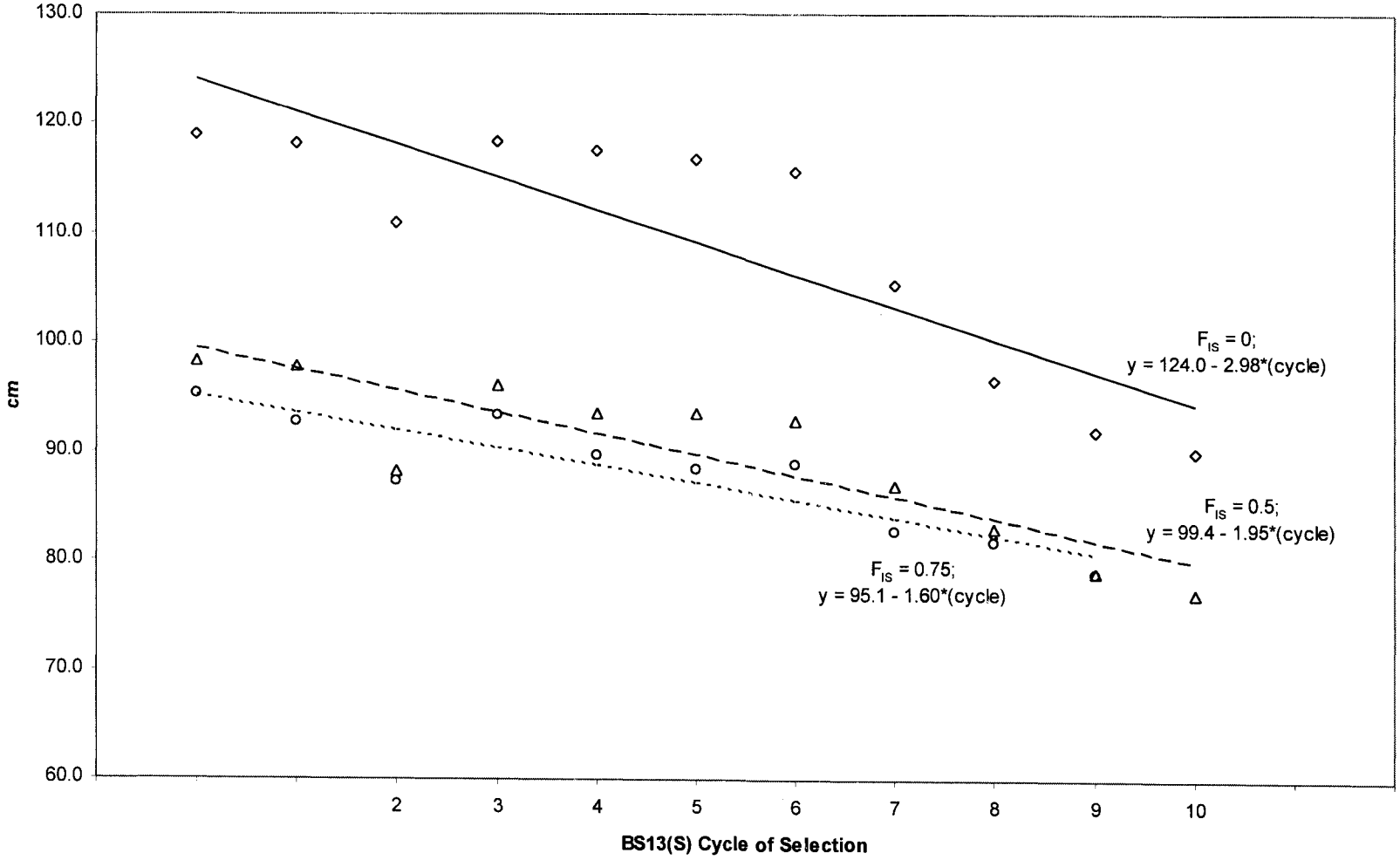
Supplemental Figure B.4.4. Observed values of BSSS, BSSS(HT)C7, and BS13(S) and predicted regressions of mean index on 10 cycles of S_2 progeny recurrent selection in the BS13(S) maize population for F_{IS} = 0, F_{IS} = 0.5, and F_{IS} = 0.75 populations.



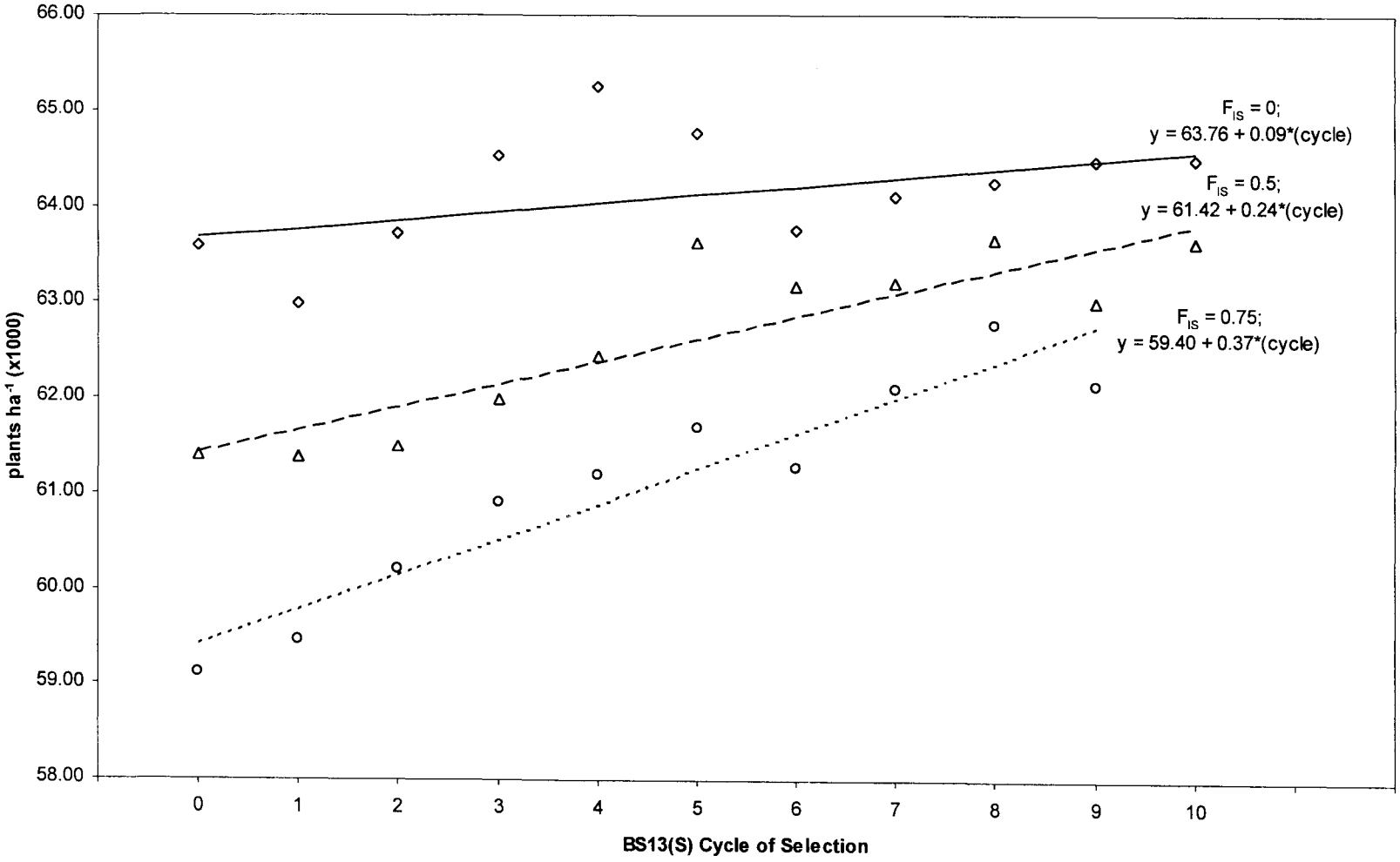
Supplemental Figure B.4.5. Observed values of BSSS, BSSS(HT)C7, and BS13(S) and predicted regressions of mean silking date on 10 cycles of S_2 progeny recurrent selection in the BS13(S) maize population for $F_{IS} = 0$, $F_{IS} = 0.5$, and $F_{IS} = 0.75$ populations.



Supplemental Figure B.4.6. Observed values of BSSS, BSSS(HT)C7, and BS13(S) and predicted regressions of mean plant height on 10 cycles of S_2 progeny recurrent selection in the BS13(S) maize population for $F_{IS} = 0$, $F_{IS} = 0.5$, and $F_{IS} = 0.75$ populations.



Supplemental Figure B.4.7. Observed values of BSSS, BSSS(HT)C7, and BS13(S) and predicted regressions of mean ear height on 10 cycles of S_2 progeny recurrent selection in the BS13(S) maize population for F_{IS} = 0, F_{IS} = 0.5, and F_{IS} = 0.75 populations.



Supplemental Figure B.4.8. Observed values of BSSS, BSSS(HT)C7, and BS13(S) and predicted regressions of mean plant density on 10 cycles of S_2 progeny recurrent selection in the BS13(S) maize population for $F_{IS} = 0$, $F_{IS} = 0.5$, and $F_{IS} = 0.75$ populations.

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Our Lord, and Good Shepard, has given my family and I so many blessings. They are countless. We live, as Americans, in a such a great country with so many freedoms we often don't even consider freedoms. To truly understand this, one must be immersed in a country less fortunate than ours, which I encourage everyone to experience. God has always provided for our family with monetary necessities and such a deep rooted love for each of us. I pray that I always give my career, my family, and my life to God our Heavenly Father.

I dedicate this dissertation along with my life in corn breeding (past, present, and future) to my loving wife, Stacie Marie (Renner) Turnbull. Stacie, I truly have depended on you for every step. It was nine years ago now that you gave me the courage (maybe even a kick!) to pursue the first round of interviews with seed companies in Nebraska. As I accepted my first job as a seed research technician we had a baby on the way and little concept of what life would be. You encouraged and supported me to leave that great company, my job with all the pay and benefits which we prospered on, and even came with me to graduate school. While I was now a father and a graduate student, once again you supported a tough decision to join the Army National Guard. This part-time guard job quickly turned into a full-blown soldier wearing boots and carrying an M-16 in Iraq as I was put on active orders in support of Operation Iraqi Freedom Feb 3. 2003 - July 30, 2004. Through all of this you supported and encouraged me along. I am so appreciative of the way you show how proud you are of me as a soldier. It is with no hesitation that I venture again with you into the unknown with a new job as a rookie corn breeder in South Dakota because

I know that you are here to support and push us as a family through this venture with love. For all of this and of what is to come I am forever grateful.

Children are so valuable as entertainers and ones to make us humble. Our children have taught me what life is worth living for. Them. Rebekah, you have always been so mature and intrigued in the life around us, I am scared to think what a super scientist you may become some day. Zachary, your energy will serve you well someday when you need to pull those all-nighters because you likely weren't prepared for the upcoming exam. Bryce, your headstrong character will carry you through so many difficult roads in life (they are endless it seems). Clinton, you are like your sister. I can already see your intriguing questions about everything around us. If you live past this destroying phase, your persistent character will be invaluable. With excitement we are expecting another child that I am anxious to learn what character you'll bring into our world. I am certain that all of you will be a huge success in each your lives and I am thankful for the opportunity to help you grow to reach your true potential.

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PhD either. However, I am grateful for your fine upbringing of me and drive you instilled in me to never be a quiter. Thank you, I pray that I can do as good a job for our children as you did for Rex, Brice, Tessa, and myself. Warren and Becky, you didn't know how serious I took it when I asked permission for Stacie's hand and you told me, "she expects the finer things in life". You are both wonderful in-laws and wonderful grandparents. I am glad that I have you and your family as family. You have helped us so many times when I couldn't be home because of school or the army.

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Last but not least, I thank Kathy, a family friend as well as style and format editor for these publications.